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STUDIES IN THE ECOLOGICAL EVOLUTION OF THE ANGIOSPERMS

By J. W. BEWS, M.A., D.Sc.

CHAPTER I

THE FOSSIL RECORD AND ITS INTERPRETATION

INTRODUCTION

BOTANISTS are accustomed to regard the fossil Angiosperm record as somewhat disappointing. In spite of continued hopes—recently further stimulated through the description by Hamshaw Thomas (1925) of angiospermous fruits from the Jurassic—that the fossil record might clear up the difficult question of the origin of the group, it must be confessed that, as yet, no very clear light has been thrown on that subject. In the Lower Cretaceous the Angiosperms are already highly differentiated, so that their beginnings must have been much earlier. We are still quite unable to decide whether the most primitive Angiosperms were closely related to the Mesozoic Cycadeoids (in which case, as Scott has recently pointed out (1924), they are to be connected with the more ancient Williamsonian tribe rather than with the Bennettiteae), or whether they are to be connected with other gymnosperms, or whether a still more ancient point of origin for them must be looked for. Opinions differ as to whether they are to be considered as monophyletic or polyphyletic in their origin. Among the systematists who have dealt with their phylogenetic arrangement there are, in addition to many differences of opinion as regards matters of detail, two widely different viewpoints. The one school regards relative simplicity in the Angiosperm flower as primitive and places the group of families belonging to the Amentiferae and similar forms—they are nearly all woody—at the base of their system. The other school regards the spiral arrangement of parts, indefiniteness of number and general lack of economy in production, etc., as primitive and considers the Ranales as coming nearest to the pro-Angiosperms. Some argue that the earliest

Angiosperms were pollinated by insects, others do not favour this viewpoint. It is not my purpose, however, to attempt, at present, to add to these discussions, since the fossil record has, so far, failed to supply convincing evidence such as would settle the matters in dispute.

Through the study of modern ecology and plant distribution, particularly in the continent of Africa, I have been led to approach the problem from an entirely different standpoint. Africa is a continent with a very stable geological history, ever since Permian times. It has not changed very much throughout the long history of the Angiosperms. Now careful comparisons within all the narrower circles of affinity, within the limits of the families, or sometimes within the limits of the larger genera, have served to show that in Africa the moist warm tropical flora is older than the flora of drier and cooler regions. The tropical forest vegetation has apparently been differentiated under conditions which have remained unchanged for an enormous interval of time, indeed since the beginnings of the Tertiary, or earlier. This differentiation has been influenced, not by any pronounced changes in climate, but chiefly by the organic environment, competition for space, etc. The plant forms include trees, mostly hard wooded and not much branched, with relatively large and usually leathery leaves, varying in height, but otherwise of a rather uniform type; large numbers of lianes, passing from the woody types to the herbaceous; large numbers of epiphytes, representing a further and more specialised stage in evolutionary differentiation; and a considerable number of mesophytic undershrubs and herbs, which are associated with the forest as undergrowth.

The evidence from phylogeny, which I have recently been examining very fully for the world's flora as a whole, affords convincing support to the view that climatic differentiation has been responsible for the production of the types of plant form adapted to more open grassland conditions, to scrub, semi-desert, and desert, and also, though this began very early, to the temperate flora as well.

PAST CHANGES OF CLIMATE

The view that the climate of the world remained more or less uniformly warm and moist from the beginnings of the Palaeozoic right down to the Pleistocene is now more or less definitely discarded. The more modern viewpoint, as expressed by Schuchert (1914), Brooks (1922) and others, recognises two great alternating types of climate. Following on periods of crustal movement and the formation

of large land areas, the general climate was cool with a marked zonal distribution of temperature, culminating, in at least four periods, in the development of great sheets of inland ice. During quiescent periods, on the other hand, the climate became warm and equable and apparently rather uniform over a great part of the world. The changes in Proterozoic and Palaeozoic times need not be dealt with, since the Angiosperms had not then appeared. In upper Jurassic times, when the earliest Angiosperms were undoubtedly already in existence, the climate of the world was warm. Schuchert points out that, at this time, the plants of Louis Philippe Land in latitude 63° S. are the same as those of Yorkshire. Whether this statement is strictly accurate or not, it can at least be said that they are very similar. Such warm conditions continued apparently for a period at least as long as the whole of the Tertiary, until the close of the Cretaceous, when there were many crustal movements, an up-building of mountain ranges and a lowering of temperatures. But there was no very extensive glaciation at this time—the only evidence of such is a local glaciation in the San Juan Mountains of Colorado—and the cooler interval was comparatively a short one. Most of the Eocene deposits, whether Lower, Middle, or Upper, indicate warm and equable conditions, and such prevailed at least through the first half of the Tertiary, or according to some authorities until towards its close, when the great ice period began to supervene.

Wegener's theory of drifting continents on a sub-fluid magma (1920, 1924) and consequent wandering of the poles and equator, while it helps to explain certain facts, yet tends to raise other difficulties. It is by no means easy to explain all the detailed phenomena of cooling and glaciation during Quaternary times on the lines adopted by Wegener. According to Wegener's theory, moreover, glaciation must always have been proceeding somewhere, unless both poles were surrounded by wide expanses of sea. This, as Brooks points out, is hard to reconcile with the extremely definite and limited glaciation which geological research has demonstrated.

Probably Wegener's theory will ultimately be combined with that recently put forward by Joly (1924) where the alternate periods of accumulation of heat and cooler conditions following on outbursts of volcanic activity and the upbuilding of mountain ranges and continents are explained by reference to the effects of the radio-activity of materials in the earth's crust. Nor is it likely that Wegener's theory can be applied in such a drastic way as he has been inclined to apply it.

THE IDENTIFICATION OF FOSSIL ANGIOSPERMS

Though Angiosperms from the Cretaceous onwards are abundant as fossils, yet from the palaeobotanical standpoint much of the material is unsatisfactory in so far as it consists mostly of leaf impressions. Several leading systematists have expressed the view that leaves, even living leaves, are, as a rule, altogether undeterminable. Nevertheless, palaeobotanists have not hesitated to apply the names of modern genera and even species to most of the fossil leaf impressions and, when occasionally they found themselves more than usually in doubt, they have suggested affinities by altering slightly the termination of modern names as *Celastrophyllum*, *Euphorbiophyllum*, *Populites*, *Sabalites*, *Leguminosites*, *Proteoides*, etc., or by using a prefix, as in *Palaeocassia*.

The number of fossil species belonging to modern genera would appear to have been extraordinarily great. Thus taking the North American species alone, from Knowlton's catalogue, we learn that somewhere about 180 species of *Ficus* are supposed to have been distinguished, together with about 40 species of *Cinnamomum*, 30 species each of *Celastrus* and *Celastrophyllum*, with another half-dozen species of *Celastrinites*, 100 or more species of *Populus* with numbers of *Populophyllum* and *Populites*, about 70 species of *Salix*, about 40 species of *Sapindus*, and 8 of *Sapindoides* with a few of *Sapindopsis*, about 60 species of *Myrica*, about 50 species each of *Aralia* and *Magnolia* and so on.

No botanist who has struggled with the many, often very polymorphic, modern species of *Ficus* can fail to admire the ingenuity of the palaeobotanists, who can distinguish two or three hundred species of the genus by leaf impressions alone. Scott, Seward and other distinguished palaeobotanists are not so confident and are inclined to approach the subject of the identification of fossil Angiosperm leaves with extreme caution. Berry (1914) who, with Knowlton and other American workers has done much to advance the subject, in discussing his own investigations on the Georgia Claiborne flora, says "The reference of *Arundo* to the grasses is positive, but in so far as its generic affinity is concerned the writer has simply conformed to palaeobotanical usage. The form classed as *Potamogeton* may not be a *Potamogeton*, although it resembles that genus very closely and is most certainly a monocotyledon of aquatic or semi-aquatic habit." And again (1924, p. 49) the same author remarks, "The use of the generic name *Arundo* is in a form sense and follows

usage. It cannot be claimed to have any especial significance as indicative of close botanical relationship."

While such palaeobotanical usages may be defended on the ground of geological convenience, from the purely botanical standpoint they are apt to give wrong impressions. The study of fossil Angiosperms, however, may be expected to pass through stages, familiar to all systematists. It is easier to increase the number of described species than to reduce them and sink a number of separately described forms in one. No doubt the time will come when a very large number of names of fossil species will be sunk as synonyms.

Some leaf forms are, of course, more characteristic and more easily recognisable than others and in several cases names given to leaf impressions have afterwards been corroborated by the discovery of specimens showing either flowers or fruits. This certainly tends to add to our confidence in the subject as a whole, in spite of the admittedly rash procedure of some palaeobotanists.

Some of the fossil flowers discovered have their structure fairly well preserved, e.g. the interesting monocotyledonous flower of liliaceous type, *Cretovarium japonicum* Stopes and Fujii, from the Upper Cretaceous of Japan, or *Combretanthites eocenica* Berry, and a few others, but it is hardly to be expected that mere impressions of flowers will yield much more definite information than those of leaves. Fruits are more often recognisable, since they are more easily preserved. Finally, we have the very important evidence from fossil Angiosperm wood. Relatively few Angiosperm woods have, so far, been described, but it is interesting, at the outset, to note that those that are known are nearly all of a tropical or sub-tropical type.

In drawing up a condensed general account of the Angiospermous fossil record, published figures and descriptions have had to be relied on, but these have been carefully consulted throughout. Accepting only the identifications that appear more or less well founded, we still have sufficient evidence to show that, before the end of the Cretaceous, the Angiosperms were very highly differentiated.

The Dicotyledons were, almost entirely, trees and shrubs and were proportionally apparently more abundant as compared with the Monocotyledons than they are even at the present time. Due value, however, should be given to the fact that woody types are more easily preserved than herbaceous, and dicotyledons than monocotyledons. The Archichlamydeae are predominant throughout among the fossil Angiosperms, but a few of the Sympetalae go back to the Cretaceous.

As already remarked, the fossil evidence does not throw much light on the rival theories regarding the origin of the Angiosperms. In support of those who favour Engler's arrangement, the Amentiferous families are very well represented at an early stage of the fossil record. The genus *Juglans* (the walnut) has existed apparently from the Middle Cretaceous to the present day. Formerly it was much more widespread than it is now. In the same family (Juglandaceae) the genus *Engelhardtia* has its characteristic winged fruits, as well as leaves, preserved. At present it is confined to South-East Asia, but during the Tertiary period species occurred in Europe and North America. The Myricales (bog myrtles) go back to the Middle Cretaceous. The genus *Myrica* throughout its geological history appears to have been—as it is now—a seashore (sand-dune) or else a rather distinctly hygrophilous type. The Betulaceae and Fagaceae are also ancient, the former being well-developed in the Upper Cretaceous of North America, and among the latter, the genus *Dryophyllum* (now extinct) being especially characteristic of the late Cretaceous and early Eocene floras of the whole world. According to Berry (1916, p. 81) *Dryophyllum* represents the ancestral stock from which the genera *Castanea*, *Castanopsis*, *Pasania* and *Quercus* took their origin, though that origin was in late Cretaceous times. The leaves of the various species of *Dryophyllum* were usually of a large simple coriaceous tropical-subtropical type.

Among the Urticales (Ulmaceae, Moraceae, and Urticaceae) the Moraceae, which at the present time are mostly tropical or subtropical, have the genera *Ficus*, *Artocarpus* and *Artocarpidium* going back to the Cretaceous.

Fruits as well as leaves of the breadfruit (*Artocarpus*) have been described by Nathorst (1890) from Greenland. According to Berry (1916) at least 15 fossil species are known. The genus *Ficus* is the largest fossil genus, including about 300 species altogether, but many are extremely doubtful as correct identifications. It appears first in the Upper Cretaceous. The elms (Ulmaceae) may be equally ancient, though their record is not so clear or certain. The Urticaceae are more herbaceous and are apparently a modern family. The fossil history of the Proteaceae has given rise to a voluminous literature, having been dealt with by Unger, Heer, Ettingshausen, Schimper, Schenck, Saporta and several others, as well as by more recent writers. Though modern members of the family are mostly South African and Australian, yet some do extend north of the equator in Australasia, Africa and America. Berry argues strongly for their former

occurrence in the northern hemisphere where, he thinks, they originated, appearing first in Lower Cretaceous times and becoming practically cosmopolitan in the Upper Cretaceous. Scott, on the other hand, gives it as his opinion (1924) that it is probable that the few genuine fossil Proteaceae are limited to Australia.

The occurrence of *Aristolochia* in the Upper Cretaceous beds of America and in the Tertiary of Europe is interesting as showing the early development of the climbing habit. Among the Centrospermae the Nyctaginaceae appear to have the most ancient fossil record.

Those who look upon the Ranales as the most primitive types of Angiosperm, connecting them with the Mesozoic Cycadophytes, can find equally good support for their views in the fossil record. The family Magnoliaceae are rich in supposed fossil remains from the Cretaceous onwards. About 60 fossil species have been referred to *Magnolia*. They are commoner in America than in Europe. The family Anonaceae, at present predominantly tropical, had the genus *Anona* in the Cretaceous of North America, but the genus *Asimina* goes back apparently only to the Eocene. The Lauraceae are supposed to include a very large number of somewhat uncertain leaf types, though fruits and seeds also occur. More than 50 fossil species of *Cinnamomum* have been described. The modern species of this genus are confined to the warmer regions, especially South-East Asia but they appear in the early part of the Upper Cretaceous in New Zealand, Australia, Central Europe, Greenland and North and South America. Such extraordinarily wide distribution of tropical types is very difficult to explain on the lines of Wegener's theory alone. The Eocene records of *Cinnamomum* include all the continents except the Antarctic and South America. According to Berry, the genus appears to have lingered as a common type in Mediterranean Europe until the changing climates that ushered in the Pleistocene caused its extinction.

Similarly the genera *Persea*, *Ocotea*, *Nectandra*, *Sassafras* and *Laurus* are also said to go back to the Cretaceous and to have been widespread, though at the present time they are mostly confined to the warmer regions of the world. The genus *Sassafras* is important because its peculiar lobed leaves and characteristic venation are very distinctive and make it easily recognisable. Existing species of *Sassafras* occur in North America and South-Western China but more than 40 fossil species have been described. At the base of the Upper Cretaceous the genus ranged from Greenland to South America.

Among the Rosales, the witch-hazel family (Hamamelidaceae) have the genera *Hamamelis* and *Parrotia* from the Cretaceous and *Liquidambar* from the Eocene beds of North America. The Leguminosae, though recorded for the Cretaceous, become abundant only in the Eocene. A phyllode-bearing *Acacia* (*A. wilcoxensis*) is described by Berry for the Wilcox (Eocene) beds. Other Wilcox genera include *Inga*, *Pithecolobium* and *Mimosites* of the Mimosoideae, *Cassia*, *Caesalpinia*, *Gleditschiophyllum* of the Caesalpinoideae, and *Sophora*, *Dalbergia*, *Canavalia* of the Papilionatae.

The Platanaceae (plane trees) have flowers and fruits as well as leaves recorded from the Cretaceous. The globular catkins are easily recognisable and have been found in the Cretaceous beds of Bohemia. The Aceraceae (maples) also have leaves and fruits in the Middle Cretaceous of North America. The family Anacardiaceae are best represented in the fossil record, as they are at present, by the genus *Rhus*, which is said to go back to the Upper Cretaceous, as also the genus *Pistacia*. In the Ilicaceae, the genus *Ilex* has more than a hundred fossil species, of which about a dozen are Upper Cretaceous. The Celastraceae have five genera in the Cretaceous and become very important in most fossil floras of the Tertiary. The genus *Celastrus* is the largest fossil genus and at one time was apparently cosmopolitan. The genus *Elaeodendron*, now confined to South Africa, had four Upper Cretaceous species, one from Australia and three from North America. The Sapindaceae, at present one of the most characteristic of the woody tropical and subtropical families, also go back to the Upper Cretaceous of North America, Greenland and Bohemia. The Rhamnaceae are equally ancient. Among the Sterculiaceae, the genus *Sterculia* was apparently well represented in the Upper Cretaceous.

The Myrtaceae are divided into the subfamilies Myrtoideae, with fleshy fruits, widespread in the tropics of both worlds, and the Leptospermoideae, with capsular fruits, mainly Australian. The genus *Eugenia* with 600-700 species is the largest in the Myrtoideae, the genus *Eucalyptus* in the Leptospermoideae. Now there is little doubt that *Eugenia* is a very ancient type. It is recorded for the (Dakota) Cretaceous beds of North America, and Cretaceous fossil wood from Natal described by Warren (1912) was found to be practically identical with the wood of the modern *Eugenia cordata*, a common subtropical very hygrophilous Natal tree. The evidence for *Eucalyptus* being equally ancient is much more doubtful. It has been recorded for Europe in Cretaceous times by Heer, Unger and Ettingshausen, and

Scott (1924) accepts the evidence as well attested (giving a figure of *Eucalyptus angusta* which shows flowers as well as leaves) yet Berry (1916) says that all the numerous Cretaceous fossil plants from North America now referred to *Eucalyptus* show characteristic features of *Eugenia* or the closely allied genus *Myrcia*. The evidence, from phylogeny and present-day distribution and all that so far has been brought to light regarding the course of ecological differentiation, would certainly support the view that *Eucalyptus* is a derivative type.

The Combretaceae, a rather characteristic family of drier subtropical regions, are not recorded earlier than the Eocene. Many apparently Araliaceous fossil leaves have been referred to the genus *Aralia*. No fewer than 50 species are supposed to go back to the Cretaceous. The genus *Panax* is also recorded for Greenland, North America, and Bohemia. Fifteen species of *Hedera* have been described for the Cretaceous of America and Europe. In the Cornaceae, the genera *Cornus* and *Nyssa* are as old as the Cretaceous. The Umbelliferae, on the other hand, are apparently modern. All the families so far mentioned belong to the Archichlamydeae and they are by far the most abundantly represented.

The Sympetalae are not so common, but they do occur even in the Cretaceous. The Myrsinaceae at present are predominantly tropical. Of the 75 fossil species of *Myrsine* seven or eight go back to the Cretaceous, mostly in America, but one occurs in Europe. Among the Sapotaceae many Cretaceous fossils both in Europe and America have been referred to the form genus *Sapotacites*, but *Mimusops* is also said to be nearly as ancient. In the Ebenaceae, the genus *Diospyros* has 180 existing and nearly 100 fossil species, no less than 17 being traced back to the Cretaceous, occurring in localities as widely separated as Australia, Bohemia, Greenland and Vancouver Island; another striking instance of wide distribution. The genus *Royena* is represented by fruits from the oasis of Chargeh in Egypt (Upper Cretaceous). Among the Oleaceae, leaves of the ash (*Fraxinus*) are recorded for the Upper Cretaceous of Greenland. The Apocynaceae, another modern tropical family, occur in the Cretaceous as species of *Apocynophyllum*. The genus *Nerium* was also recorded by Saporta from the Upper Cretaceous of Westphalia, but Berry considers this a mistake, the genus in question being a member of the Myrtaceae and not *Nerium*. In the Boraginaceae the genus *Cordia*, an admittedly primitive phylogenetic type, at present tropical or subtropical, appears to go back as far as the Cretaceous in America. The bulk of the family is relatively modern. Among the Caprifoliaceae the genus

Viburnum has been recorded from the Cretaceous of Greenland and North America. Many other families, which we have not mentioned, go back as far as the Eocene.

Among the Monocotyledons, the palms were common during the Cretaceous and still more so throughout the Tertiary. Their cosmopolitan distribution as fossils contrasts once more with their restricted, mostly tropical or subtropical, distribution at the present time. Their wood is frequently well preserved from the Cretaceous onwards. The evidence for the occurrence of the grasses is more uncertain, though the reed grasses *Arundo* and *Phragmites*, or types like them, occurred in the Cretaceous of Greenland and North America. Of the Typhaceae *Sparganium* appears to be equally ancient, fruits as well as leaves being preserved. Among the Araceae the aquatic genus *Pistia* is found in the Upper Cretaceous beds of North America and Europe. In the Liliaceae leaves that have been referred to the climbing genus *Smilax* are found in the Upper Cretaceous of Bohemia. The genus *Dracaena* and other arborescent forms are found in various Tertiary beds. On the whole, however, the Monocotyledons are poorly represented and the fossil evidence throws no light on their origin or on their relationship to the Dicotyledons.

THE ECOLOGICAL INTERPRETATION OF THE FOSSIL ANGIOSPERM RECORD

Ecological deductions from the fossil Angiosperm record have usually been made to depend on the assumed correctness of the identifications. Arguments have then been based on the known ecological behaviour of modern representatives of the same genera or species. In many cases and with due precautions, as we have seen, this procedure is doubtless perfectly justifiable. At the same time, it does admit of much destructive criticism from those who do not believe that the majority of fossil Angiosperm leaf impressions are recognisable or capable of being referred to modern genera.

This difficulty, however, from the purely ecological standpoint (which is the important one when past climates and their relationship to plant distribution are being considered) can to a large extent be avoided by adopting another line of procedure. Morphological comparisons of the Angiosperm fossil plants can be made, not with modern individual genera or species, but with modern types of vegetation. To do so successfully, statistical methods must be adopted.

The credit of introducing ecological statistical methods in determining the climatic relations of floras is due particularly to Raunkiaer.

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His system of classifying the life forms of plants is now well known, thanks largely to an explanatory article by W. G. Smith which appeared in the first number of the *Journal of Ecology* (1913). It is, of course, difficult to apply Raunkiaer's actual system to fossil plants, since, with very few exceptions, they all belong to his one class of Phanerophytes (Trees and Shrubs) and the fossil record gives little information regarding the relative size of the woody plants to which the leaves belonged. The abundance of trees and shrubs, after making due allowance for their greater likelihood of being preserved, shows that the climate of most parts of the world, from the beginning of the Cretaceous and earlier right down to the close of the Tertiary, was what Raunkiaer calls a "Phanerophytic climate."

This does not, of course, mean that there were no herbs, anymore than a phanerophytic climate implies a total absence of herbs at the present time.

STATISTICAL COMPARISONS; LEAF SIZE

The Phanerophytes were originally subdivided by Raunkiaer into evergreen and deciduous classes and further, according to the degree of protection of the renewal buds, depending on decrease in size of the whole plant. The majority of the fossil leaves appear to have been of the evergreen type, though it is not always easy to be certain on this point. In later papers Raunkiaer gave attention to variations in leaf size. The most satisfactory method of doing so is to estimate the average total area of the surfaces of the individual leaves of each species. When very large numbers are being dealt with, however, and especially when published descriptions have to be relied on, the calculation of leaf areas becomes very laborious. Some published descriptions omit reference to leaf size altogether or use vague general terms, but usually the average length and the average width in the widest part are given. A rough idea of leaf size can be obtained from such linear measurements.

In statistics dealing with the South African flora (Bews, 1925), four main classes of leaves were recognised—(a) simple leaves over 3 in. long, (b) simple leaves 3-1 in. long, (c) simple leaves less than 1 in. long, and (d) compound leaves. Average measurements were taken in each case and the English linear system of measuring was adhered to since it is used throughout the *Flora Capensis*. Apart from this, however, the three sizes (3 in. or 7 cm., 3-1 in. or 7-2½ cm., and less than 1 in. or 2½ cm.) have proved very convenient.

In order that the fossil flora may be compared as regards leaf size with modern types of vegetation, statistics of the same nature have been compiled from various published monographs and these are set forth in Table I. Only the more extensive monographs have been made use of, since, where less than 50 fossil species have been described, the numbers have been considered too few to yield statistical percentage results which can be compared with modern floras.

TABLE I
Fossil Angiosperms

Locality and geological horizon	Authority	Total No. dealt with	Leaves simple over 3 in. %	Leaves simple 3-1 in. %	Leaves simple under 1 in. %	Leaves compound %
Eastern Gulf region						
Upper Cretaceous	Berry	138	54	29	7	10
South Carolina						
Upper Cretaceous	Berry	50	64	18	6	12
Laramie, Denver						
Upper Cretaceous	Knowlton	75	57	26	3	14
Wilcox group						
Lower Eocene	Berry	262	47	17	5	31
Claiborne flora						
Middle Eocene	Berry	58	62	10	2	26
Jackson flora						
Upper Eocene	Berry	89	57	16	4	23

While the statistics given in Table I do not depend on the identifications of the species concerned, yet they still have faults due to the necessary imperfections of the fossil record. One or two of these may be referred to briefly.

(a) The preserved specimens may not represent average samples of the species to which they belonged. It is well known that young leaves differ from old, juvenile forms from the adult, leaves on coppice shoots from those on main stems or branches, shade-leaves from sun-leaves. This difficulty must always be kept in mind when individual identifications are being considered, but statistical methods and percentages of fifty or more are not likely to be affected much by some specimens being non-typical of the species to which they belonged.

(b) The percentages of compound leaves as given in the table do depend, to some extent, on the accuracy of their supposed determinations. Compound leaves are only occasionally preserved complete and usually only separated leaflets occur, especially in the case of pinnate leaves. Of course their exact relationships may be in doubt and still they may be recognised as at least being compound-leaved forms. The matter is not of any great importance.

(c) The most serious difficulty in the ecological interpretation of the fossil record and in seeking to correlate past climates and vegetation lies in the fact that the whole preserved collection of fossil leaves in any particular place may not have been, and indeed very likely was not, typical of the vegetation as a whole. The leaves of trees and shrubs would be more easily preserved than those of herbs, the vegetation of stream banks, river banks and estuaries would be more likely to be found abundantly than the vegetation of drier areas away from water, mesophytic or hygrophilous types would naturally be more common as fossils than extreme xerophytic types.

The importance of this difficulty has been generally recognised and, if anything, has been perhaps over-emphasised. It is unnecessary to go to extremes and declare that because the fossil record is incomplete it is, therefore, worthless; that because the vegetation of desert regions would not be so easily preserved, therefore its absence from the fossil record not only makes it possible but even probable or practically certain that desert types are just as ancient as the mesophytic types which do occur so abundantly. Caution is a very desirable thing, but it can be carried too far. We can continue to interpret the past in terms of the present, and our safest guide is what can be learned from the ecological behaviour of modern types of vegetation. Experience gained in dealing with the ecology of the subtropical vegetation of South Africa has shown, beyond any doubt, that even in the hygrophilous habitats mentioned (stream banks, river banks, lagoons and estuaries) a dry climate is not without a pronounced and easily recognisable effect. I have dealt with this question in detail elsewhere (1925). It is true that along stream and river banks hygrophilous trees and shrubs can extend into drier climatic areas, but even in such situations the effects of increasing aridity are soon apparent. South African tree types like *Xymalos*, *Bridelia*, *Macaranga*, *Voacanga*, *Rauwolfia*, *Eugenia cordata*, etc., which are closely similar to the average form found abundantly as fossils from the Cretaceous onwards, occur along streams, it is true, but only in the moister and warmer climatic areas. In the drier areas, they are replaced by quite different types like *Acacia*, *Rhus*, *Zizyphus*, *Combretum*, etc., which also grow along the stream and river banks in such areas.

If the climates of Cretaceous and Eocene times had been as dry as the climate of, say, the South African Karroo is now, there appears to be no reason why the woody vegetation of the river banks and estuaries and the preserved fossils should not have recorded the fact.

Since herbaceous forms have not been commonly preserved, we shall compare the fossil types only with modern trees and shrubs. To enable us to reach conclusions so far as leaf size is concerned similar statistics for modern types of vegetation are given in Table II.

TABLE II
Modern Trees and Shrubs

Ecological type	Total No. dealt with	Leaves simple over 3 in.	Leaves simple 3-1 in.	Leaves simple under 1 in.	Leaves compound
		%	%	%	%
South Africa as a whole	800	20	40	9	31
South African hygrophilous subtropical type	60	75	19	0	6
South African mesophytic forest type	150	32	47	3	18
South African xerophytic parkland and scrub types	500	11	34	13	42
British temperate type	100	20	36	28	16

The figures given in Table I show that the early Angiosperms while exhibiting a fair amount of differentiation as regards leaf size were predominantly of a large-leaved type and comparison of the two tables shows that the Cretaceous and Eocene vegetation approached nearest to modern warm moist (hygrophilous) forest vegetation. The percentage figures show that the early vegetation differed markedly from the modern xerophytic scrub vegetation or open parkland vegetation on the one hand and from modern temperate woody vegetation on the other. I have shown in my work on *Plant Forms* (1925) already referred to, that the South African xerophytic scrub and "Tree Veld" vegetation is to be considered relatively modern and derivative, basing my conclusions on the evidence from phylogeny and modern distribution. The fact that there is a marked increase in the percentage of compound-leaved forms in such derivative vegetation may be significant and it is, therefore, worth noting that the percentage of such compound-leaved forms in the fossil record is higher in the Eocene than in the Cretaceous.

LEAF MARGINS

While leaf size is one of the most important features to be correlated with climate, there are other characters, which are also worthy of attention. Bailey and Sinnott (1915) are quoted by Berry (1916, p. 138) as having formulated a method of approximating climatic factors by a study of the percentages of dicotyledonous leaves with entire and with toothed margins. The Wilcox flora, which is the richest in records, in so far as it is represented by leaves and leaflets,

comprises 264 species with entire and 64 species with toothed margins, or 82.6 per cent. of the former and 17.4 per cent. of the latter. This percentage of entire-leaved forms shows remarkably close agreement with various modern tropical floras e.g. Ceylon (80 per cent.), Manilla (81 per cent.), West Central Africa (81 per cent.), Queensland (82 per cent.), New South Wales (82 per cent.) and Florida (83 per cent.) but differs entirely from modern temperate floras. The British temperate trees and shrubs, for instance, only have about 30 per cent. with entire leaves. It is, of course, not so obvious why a simple character like toothed margins should depend on climate, but if it does not depend directly on climate, but rather on phylogenetic history independently of the influence of the environment, it is all the more valuable as an indication of the ancient character of the tropical tree form, which, in this respect as well as others, agrees so closely with the ancient fossil Angiosperms.

LEAF TEXTURE

Berry (1914, p. 67) calls attention to the presence of numerous fossil Angiosperms with coriaceous leaves, and says that this is believed to be due to insolation and the pseudo-xerophytism of swamp habitats rather than to any approach to aridity. As a matter of fact, however, the leaves of most evergreen species of trees, even when they grow in the moistest types of tropical rain forest, show some degree of leathery texture and are only rarely quite thin and membranous. Species with coriaceous leaves are by no means confined to swamp habitats. *Xymalos monospora*, for instance, is a dominant hygrophilous Natal tree with distinctly coriaceous leaves. It is found in the wettest types of forest and nowhere else, but the soil in which it grows is well enough aerated and the character of its leaves, as in the case of many other similar species, cannot be explained by any theory of physiological drought or pseudo-xerophytism. Coriaceous-leaved species are, of course, also found under drier conditions and it is not denied that this leathery texture may be looked upon as a xerophytic response. The term "xerophyte" is one which often leads to misapprehensions. It is sometimes used purely in a morphological sense, sometimes, on the other hand, it is applied to habitat as well. Now the possession of coriaceous leaves does not necessarily imply dry conditions and if they occur abundantly in situations where plenty of water is available, it is clear that an explanation must go deeper. It is not enough to talk vaguely of xerophytism.

It seems to me that a considerable amount of light is thrown on the subject by considering more carefully the whole question of the water supply of the leaves and its relationship to the water-conducting power of the wood. Farmer (1918) devised a method of measuring what he called the "specific conductivity" of woods and showed in a general way that evergreen species are less efficient in raising water quickly to their leaves than are deciduous species. In Natal, recently, we have applied his method to a considerable number of species and gradually it has become apparent that increased efficiency in water conduction has only been reached by dicotyledonous trees after a long period of evolutionary development. The relatively primitive evergreen tropical or subtropical forms are, as a rule, not able to pump up water very quickly. Moreover, further experiments on the rates of drying out of their leaves and on their "water deficits" under varying conditions have shown that some of them begin to suffer after only brief periods of bright sunshine and relative aridity. Though plenty of water may be available at their roots, it cannot be supplied rapidly enough to their leaves. Such species, of which *Xymalos monospora* is an example, are, therefore, confined to the wettest areas and, even there are occasionally in danger. Hence probably the necessity for having coriaceous leaves. Even tropical rain forest is not uniformly and continuously equally moist. There are short, dry intervals and leathery-leaved trees are characteristic, especially in the upper canopy.

Some coriaceous-leaved trees, which have low rates of water conduction, occur, not only in wet forest, but in drier places as well. These show greater powers of withstanding a lowering of the leaf water content. *Ptaeroxylon utile* is a good example of this class.

Finally, the more derivative, more highly evolved species of trees which occur in drier subtropical areas or in colder (temperate) regions often have thin membranous leaves, but, at the same time, show a much higher rate of water conduction. Such forms tend to be more or less regularly deciduous in regions where a pronounced resting season is brought about either by dry conditions (dry winters) or by cold conditions (cold winters).

The figures given in Table III are selected from numerous experimental observations made on the Natal flora and on exotic species cultivated there.

TABLE III
Water Conduction in Trees¹

Tropical or subtropical mesophytic or hygrophilous evergreen types	Spec. conductiv- ity	Xerophytic subtropical or temperate deciduous types	Spec. conductiv- ity
<i>Podocarpus henkelii</i>	12-16	<i>Magnolia</i> sp.	20-40
<i>Xymalos monospora</i>	10-17	<i>Platanus occidentalis</i>	38-75
<i>Eugenia cordata</i>	12-13	<i>Amygdalus persica</i>	35-66
<i>Avicennia officinalis</i>	17-21	<i>Heteromorpha arborescens</i>	27-56
<i>Rhamnus prinoides</i>	12-19	<i>Ficus capensis</i>	70-80
<i>Gardenia globosa</i>	19-25	<i>Cordia caffra</i>	50-90
<i>Ptaeroxylon utile</i>	10-22	<i>Maesa rufescens</i>	80-100

The differences in the rates of water conduction between the leathery-leaved evergreen types and the thin-leaved or deciduous types are sufficiently striking and in general it would appear that the coriaceous texture of leaves in moist-tropical species is probably to be explained by their relative inefficiency in water conduction. The significance of the presence of so many coriaceous leaves among fossil Angiosperms is, therefore, two-fold. (1) It serves to connect the earlier types of plant with tropical or subtropical modern hygrophilous or mesophytic types, as before, and (2) it is not necessarily to be explained by the pseudo-xerophytism of swamp habitats or by any marked approach to aridity but simply by the same lack of efficiency in the water-conducting power of the wood which is found to-day in tropical forms. It is reasonable to suppose that in such basic physiological processes, as in other connections, evolutionary development has gradually led to increased efficiency.

STRUCTURE OF THE WOOD

With fossil forms, of course, it is impossible to carry out experiments on the rates of water-conduction, but their woods are to some extent available though relatively few examples have so far been described. As in the case of the leaves, the giving of the names of modern genera or species to fossil woods, the determining of their systematic positions and relationships to modern forms is a difficult matter and is not necessarily the most important task to be undertaken by the palaeobotanist. Apart altogether from their identification, much may be learned from a careful study of their structure and by ecological comparisons with modern types. Unfortunately, very little work of this kind has so far been done.

The oldest known fossil dicotyledonous woods are of Lower

¹ The figures have been taken from unpublished results obtained partly by Dr R. D. Aitken and partly by Miss Sheila Maritz.

Cretaceous age and have been described by Dr Marie Stopes (1913, 1915). There are five genera with one species in each. In four of them, *Aptiana radiata*, *Cantia arborescens*, *Sabulia scottii*, and *Hythia elgari*, the rather small vessels, which vary from 20–70 μ in diameter, would suggest that water conduction was not very efficient, but the fifth, *Woburnia porosa*, has large vessels 350 μ in diameter. The last mentioned, however, agrees in structure with the tropical Diptero-carpaceae. Some tropical species, especially those which tend to become lianes, do have large vessels. Fairly extensive experiments carried out in Natal have shown us that the rate of water conduction is not to be correlated merely with the total area of the lumina of the conducting elements, in proportion to the whole area of the woody stem in cross-section. The rate of water conduction also depends on the nature of the conducting elements themselves and particularly on the characters of the pits, pores or perforations connecting the separate elements with one another. There is room for much further work on woods from the standpoint of efficiency.

The affinities of the other Lower Cretaceous fossil woods described by Dr Stopes are undetermined, though, according to Scott (1924), *Aptiana* has been confidently placed in the family Ternstroemiaceae (to which the familiar coriaceous-leaved Camellias belong) by two Dutch writers, Profs. Janssonius and Moll.

Other woods of Upper Cretaceous age have been described from Japan by Stopes and Fujii and by American writers from North America. Their affinities with relatively primitive hygrophilous or tropical families are indicated in a general way by the names that have been assigned to them (*Saururopsis*, *Jugloxylon*, *Populocaulis*, *Fagoxylon*, *Sabiocaulis*, *Dombeyoxylon*, *Laurinoxylon*, *Ficoxylon*, *Ulinoxylon*, *Perseoxylon*, *Elaeodendroxylon*, *Ebenoxylon*); but the total number that have been described is very small as compared with the large numbers of leaf impressions that have been dealt with.

The fossil woods should be studied, not only as regards their conducting elements and probable efficiency in water conduction, but also as regards the development of medullary rays and other parenchymatous storage tissue in response to the necessity for providing for a resting season. Tropical woods from moist regions are usually hard-woods. Softer woods are produced in regions where dry or cold seasons lead to a more or less prolonged resting season. Indeed the morphological changes brought about in woody species by the advent of seasonal climatic differentiation (the alternation of a favourable warm moist growing season with an unfavourable dry

or cold resting season) are very varied and are of the utmost importance in any analysis of the course of ecological evolutionary history.

From this standpoint, attention has been directed to the presence or absence of well-marked annual rings, though this is only one, and in many ways not the most important, feature to be studied. There are growth rhythms in plants growing under more or less uniform and continuously favourable conditions which may be, to some extent, independent of external climatic changes, and successive rings of growth in woody stems may not be annual or even seasonal rings.

The presence or absence of clearly marked annual rings is not of course to be neglected (and in the fossil woods described they are not, as a rule, well marked) but in seeking to correlate ecological behaviour with climate there are many other morphological features to be taken into consideration as well. Until more work is done on the subject, however, it is impossible to draw any more definite conclusions than those tentative ones outlined above.

In conclusion, it may be said that the fossil evidence as regards the past history of the Angiosperms, incomplete and unsatisfactory though it is in many respects, yet, when its more general features are analysed, does lend strong support to the view that warm moist conditions were, for a very long period, much more widespread than they are now, and further, that the early Angiosperms were similar ecologically to the types now found in moist tropical and subtropical areas. They were differentiated in the same way as modern tropical mesophytic floras but they showed only slight indications of the influence of drier or colder conditions.

The fossil evidence, therefore, so far as it goes, supports the views already outlined, which depend primarily on the study of the phylogeny and distribution of modern vegetation. The whole subject of the ecological evolutionary history of plant forms, I am convinced, is full of very interesting possibilities.

SUMMARY

i. The study of fossil Angiosperms has made considerable progress during recent years, particularly through the work of Berry, Knowlton, and others in America. Most of the fossil remains consist of leaf impressions and the determining of their exact affinities must always be difficult. The fossil evidence has not as yet thrown much light on various rival theories regarding the origin of the Angiosperms. A condensed account is given of the identifications that appear more or less well founded.

2. In seeking to correlate the fossil record with past climates, ecological comparative methods are adopted and the fossil remains are compared in groups statistically with modern types of vegetation.

3. The features selected for comparison are (i) leaf size, (ii) leaf margins, (iii) leaf texture, (iv) structure of the wood, and in each case it is shown that the earlier fossil Angiosperms were closely similar to the types now occurring in moist tropical and subtropical areas.

4. The ecological interpretation of the prevalent coriaceous texture in the leaves of both fossil and modern tropical trees is discussed with reference to experimental work carried out in Natal on the water relations of various species. Leathery texture and a certain degree of "xerophytism" generally in the leaves of many ecologically primitive types of tropical hygrophilous trees are correlated with relative inefficiency in their power of water conduction through the wood.

NOTE. The manuscript of this chapter was submitted to Prof. Seward, and I am much indebted to him for certain helpful criticisms. It is only fair to add that with regard to the identification of the fossil Angiosperms he is inclined to adopt even a more cautious attitude than I have found necessary. The statistics and comparisons given in the later chapters of the book are not, of course, much affected, since they do not to any great extent depend on identifications.

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(To be continued)

MYCORRHIZA

By M. C. RAYNER

CHAPTER IX

"Mycorrhiza" in Bryophyta: fungus infection in Liverworts; Neméc; Stahl; Gallaud; Cavers; Ridler; Bernard; Magrou; the characters of the fungi concerned—Infection in Mosses—Mycorrhiza in the Pteridophyta; Equisetales—Lycopodiales—The gametophyte of *Lycopodium*; historical: Treub: Bruchmann: Lang—*Psilotum*: Shibata—The Sporophyte of *Lycopodium*—Ophioglossales—Filicales; Marattiaceae—Filices; fungus infection in Osmundaceae, Gleicheniaceae and Cyatheaceae—The absence of mycorrhiza in Polypodiaceae—New records of its occurrence in *Aspidium* and *Pteridium*.

Bryophyta.

THE regular occurrence of mycelium in the tissues of members of Bryophyta has long been known. There appears to be little doubt that the relation is frequently of similar biological nature to that in mycorrhiza and the use of this term to describe it has been sanctioned by usage, although it involves a very loose use of words and appears to the writer to serve no useful purpose.

The history of research on the subject reproduces in miniature that on mycorrhiza proper, i.e. it shows an earlier period of isolated observations and speculations leading gradually to the development of a more critical type of experimental investigation. Gotsche and Schleiden (1843) had noticed spiral threads in the cells of *Priessia*, the fungal character of which was afterwards recognised by Schacht (1854) and by Gotsche himself in 1858. Another early record was made by Leitgeb (1874-1881) who described fungal infection in the young sporogonium of *Ptilidium ciliare*. Janse (1897) observed it in *Zoopsis*, a tropical member of Jungermanniaceae native in Java.

Neméc (1899) recorded the presence of mycelium as a regular occurrence in the leafy members of Jungermanniaceae, of which all the species examined, with the exception of *Jungermannia tridentata*, were found to be infected. Discussing the incidence of infection, he concluded that it was dependent on habitat, and mentioned the case of *Lepidozia reptans*, a species showing typical infection in humus-rich soil in shady situations but found growing on clay soils entirely free from mycelium. Describing the infection of the rhizoids and penetration of the neighbouring stem tissues in *Calypogeia*

trichomanes, Neméc summed up in favour of the existence of a reciprocal relation as follows:—

Man könnte die zäpfchenformigen Fortsätze vielleicht als Haustorien deuten, welche der Pilz in die Zellen der Wirthspflanze einsendet, um Nährstoffe aus ihnen saugen zu können. Es ist jedoch anderseits ebenso möglich, dass die Wirthspflanze die Pilzhyphen zu derartigen Gebilden reizt, um an einer grossen Oberfläche und bei inniger Berührung möglichst leicht Stoffe entnehmen zu können.

The same author recorded mycelium in the rhizoids of *Kantia trichomanes*, *Lepidozia reptans* and *Lophozia bicornata*. In *Kantia*, the mycelium was believed to be that of *Mollisia jungermanniae*, an Ascomycete with small bluish green apothecia, often found on the thallus. Neméc observed that infected cells in *Kantia* retained their contents, the nuclei placing themselves in close proximity to the invading hyphae.

In members of Jungermanniaceae infection is usually conspicuous in the rhizoids, from the proximal ends of which interweaving branches form a pseudo-parenchymatous tissue whence outgrowing hyphae penetrate the stem. While Neméc noted that fungal infection was general in this group of Liverworts, he believed it to be absent from members of Marchantiaceae, even when growing in close proximity to infected species. Stahl (1900) attempted to correlate the incidence of infection in the Hepaticae with his theory of nutrition in mycotrophic plants. He identified the members of Jungermanniaceae and Marchantiaceae respectively as sugar-containing and starch-containing forms, and proposed to investigate the possibility of a parallelism between fungus-infection and the water-balance among Liverworts. Unfortunately for Stahl's hypothesis, the supposed differential behaviour of members of the two groups in respect to infection was not confirmed, and evidence was soon forthcoming that "mycorrhiza" formation was as frequent a phenomenon in Marchantiaceae as in Jungermanniaceae. Indeed, the presence of mycelium in the rhizoids of *Marchantia* and in those of the common Liverwort *Lunularia vulgaris* had already been noted by Kny (1879) who observed also that infection extended to the ventral parts of the thalli when growing on a substratum rich in humus.

Beauverie (1902) noted the presence of mycelium in the thallus of *Fegatella*, another member of Marchantiaceae, and believed the fungus present to be related to *Fusarium*. Golenkin (1902) added fresh records for the Marchantiaceae, describing endotrophic infection in *Marchantia palmata*, *M. palmacea*, *Priessia commuta*,

Targionia hypophylla, *Plagiochasma elongatum* and *Fegatella conica*. This author compared the endophytes with those of *Neottia* and *Lycopodium*, and suggested that the infected tissue functioned for water-storage. Against this view Cavers (1903) cited his own observations on *Fegatella* and *Monoclea*, both typically hygrophilous forms. Moreover, the thallus of the former contains well-developed mucilage tissue for the storage of water.

To the genera of Jungermanniaceae recorded by Nemèc as mycorrhiza-formers, Cavers added the names of *Cephalozia bicuspidata*, *Scapania nemorosa*, *Diplophyllum albicans*, *Plagiochila asplenoides*, *Bazzania trilobata* and *Porella platyphylla*, in all cases the degree of infection increasing with the amount of humus in the substratum. *Monoclea forsteri*, a New Zealand species, was also found to be heavily infected.

In every plant examined, vertical sections of the thallus showed a sharply defined mycorrhizal zone, consisting of from two to four layers of cells densely filled with branching fungal hyphae. This zone is confined to the thicker median portion of the thallus and extends to within a short distance of the growing point.

Gallaud (1905) held that the endophytes of Liverworts were so specialised in character as to form a distinct group, and described the intracellular distribution of mycelium and the development of vesicles and sporangioles. He also put on record the irregularity of infection observed in *Pellia*:—"Dans une même station de *Pellia epiphylla*, tous les thalles ne sont pas infestés, et ceux qui le sont le sont inégalement, sans qu'il soit possible, d'ailleurs, d'établir entre eux d'autre différence qu'on puisse nettement attribuer à l'infection." In general, he concluded that fungus infection was widely distributed in Hepaticas, alike in Marchantiaceae and in Jungermanniaceae, and he believed that it was limited to the gametophyte generation. It was absent from or very rare in the region of the thallus near the sporogonium.

Humphrey (1906), investigating the development of *Fossombronia longiseta*, a member of a genus intermediate in position between the thalloid Jungermanniaceae and the higher foliose types, noted the occurrence of tuberous swellings on the stems. Detailed examination of the tissues in these stem enlargements revealed in every case the presence of mycelium. The hyphae were restricted almost entirely to the stem and rhizoids, the latter sometimes exhibiting lateral swellings suggesting the formation of short branches. The existence of a causal relation between infection and tuberisation

was not investigated, and there is as yet no information as to the character of the fungus in *Fossombronia* or its biologic significance to the thallus.

In view of the formation of tubers by other Liverworts—they have been recorded in *Geothallus tuberosus*, *Riccia perennis*, *R. bulbifera*, *Anthoceros tuberosus*, *A. phymatodes*, *Petalophyllum preissia*, while Goebel described and figured them in *Fossombronia tuberosa*, and Howe had noted their appearance in *F. longiseta*—more information respecting the biology of infection will be awaited with interest.

As might be expected from its nature, the evidence is inconclusive concerning the physiology of infection in Liverworts. The amount of experimental data is scanty. Cavers grew spore cultures on sterilised soil and believed that development was more vigorous when mycelium was present. In control cultures he noted also that infection took place more readily from soil containing abundant humus. In general, observers have tended to regard infection as a symbiotic relation enabling the host to assume a partially saprophytic method of nutrition. In respect to the distribution of mycelium and restriction of infection observed in Liverworts, it is worth recalling the fact that Czapek (1889) had recorded the presence of an antiseptic substance, *sphagnol*, in the cell-walls of many members of Hepaticae.

There is a long gap in the records after 1906 and subsequent contributions to the knowledge of fungus infection in Liverworts fall well within the modern period. Ridler (1922) confirmed Gallaud's observations on *Pellia* in respect to the irregular distribution of infection and believed it to vary with the age of the thallus rather than with the habitat. In fronds showing the typical condition, mycelium was found to be localised to the rhizoids and the thicker part of the thallus forming the midrib—"the upper two or three layers, including the upper epidermis, remains free from hyphae."

Gallaud had described the morphology of the endophyte in *Pellia*; main trunk hyphae of large diameter bearing vesicles and sporangioles; while the presence of arbuscules, although not recorded, is implied in that of the latter organs. Ridler (1923) corroborated these observations and also described and figured the arbuscules composed of "very fine and profusely branching threads" which completely filled some cells of the thallus with a network of mycelium. The relation of these structures to the so-called sporangioles was well shown in the figures supplied by this author.

Nicolas (1924) has recently added a new record for *Lunularia*, describing regular endotrophic infection in certain thalli bearing

antheridia, although mycelium was absent from neighbouring sterile plants. As is well known, the formation of sexual organs by this common Liverwort is an exceptional occurrence, but Nicolas' attempt to establish a causal connection between the two phenomena was unsuccessful inasmuch as he subsequently discovered antheridia-bearing plants free from mycelium.

Certain recent observations on an Indian species of *Marchantia* are of interest. It was noted by Chandhuri and Rajarum (1925) that vigorous plants of *Marchantia nepalensis*, collected in the neighbourhood of Lahore, invariably showed fungus infection of the thalli. The mycelium was confined to the gametophyte and restricted to a zone of tissue below the air canals.

Isolation experiments yielded a non-sporing mycelium which readily invaded fresh gemmae giving rise to the characteristic infection. The endophyte was cultivated on various artificial media and thrived on those with a reaction of $\text{pH } 6.6$ to 7.0 . Deprived of maltose, the mycelium ceased to grow, whereas withdrawal of asparagin produced little effect. It was inferred that the organism depended upon its host for a supply of carbohydrates. Comparative cultures of infected and uninfected *Marchantia* thalli on filter paper or sterilised soil showed that those lacking mycelium developed normally, but died off without producing sporophytes. It was concluded by the author that the condition in this species of *Marchantia* is one of reciprocal symbiosis, infection by a specific fungus being essential to full development of the green plant.

Among the more important papers published by Noël Bernard in the course of his work on Orchid mycorrhiza was one dealing with the evolution of plants in relation to symbiosis—*L'Évolution dans la Symbiose* (Bernard, 1909), in which the author elaborated his thesis that the advanced degree of adaptation shown by certain members of the Bryophyta to symbiotic relations with fungi might provide a clue pointing to the origin of vascular plants from members of this phylum.

The hypothesis was based mainly on Bernard's comparative observations on the relation of tuberisation to fungus infection, together with Treub's researches on the comparative embryology of the Lycopodiaceae, as a result of which, the latter observer had been led to the view that living Vascular Cryptogams were descended from plants resembling certain Bryophytes—"quant à l'essentiel aux Muscinées actuelles (plus particulièrement aux Hépatiques)" (Treub, 1890).

With the intention of providing experimental evidence bearing on this evolutionary theory, a study of the relations in *Pellia* was undertaken by Magrou (1925). The account contributed recently by this observer provides a consistent explanation of the irregularities of infection observed in this common Liverwort and his observations on the distribution of mycelium in thalli of *Pellia* growing under natural conditions are in agreement with those on the same subject made earlier by Bernard and recorded for the first time in this paper. In particular, Bernard had noted that strongly growing fertile fronds were immune to infection up to the period of spore dispersal, becoming susceptible to infection subsequently. Magrou has confirmed this observation and recognised the presence in early spring of at least three generations of superimposed branches in any actively growing colony of *Pellia*, viz. old brown thalli with scars of sporogonia of the preceding year; younger thalli, dark green in colour, that have just produced sporogonia; and still younger fronds of bright green colour bearing antheridia and archegonia. The oldest fronds showed profuse infection by the characteristic endophyte, with abundant evidence of the effective control exerted by the host, by the gradual conversion of arbuscules to sporangioles within the cells of the thallus.

In the younger generation of fronds, infection was found to be less pronounced; in every case, a zone of tissue about the base of the young sporogonium exhibited immunity to infection by the rapid destruction, not only of haustorial branch systems, but of the main hyphal branches. This protective zone included the rhizoids developing on the ventral side of the same region. In the youngest generation of branches bearing sexual organs, the immunity secured in this way was even more conspicuous. Except in those cells most remote from archegonia, the mycelium showed complete degeneration, following so rapidly upon penetration as to cause almost complete inhibition of arbuscule formation. This immunity to infection was limited to tissues neighbouring living archegonia and actively developing sporophytes, and came to an end when these organs completed their development or became disorganised; following dehiscence of the capsule, mycelium rapidly invaded the surrounding tissues of the thallus. The endophyte was of the characteristic mycorrhizal type, producing vesicles and arbuscules (Fig. 57 A, B). Sowings of spores upon infected soil provided young gametophytes subjected to infection at an early stage of development. Observations on infected cells showed that the mycelium caused destruction of the chloroplasts, leading to the browning of tissue

commonly recorded. It resulted also in marked arrest of growth, transferred ultimately to branches developing from islets of meristematic tissue, thus producing a characteristic tufted habit of growth.

To estimate correctly the exact rôle of the endophyte involves, in this case as in others, the separation and observation of each member of the association in pure culture, and their synthesis under controlled conditions. Inasmuch as the endophyte of *Pellia* has hitherto resisted isolation, it has been possible to draw only limited

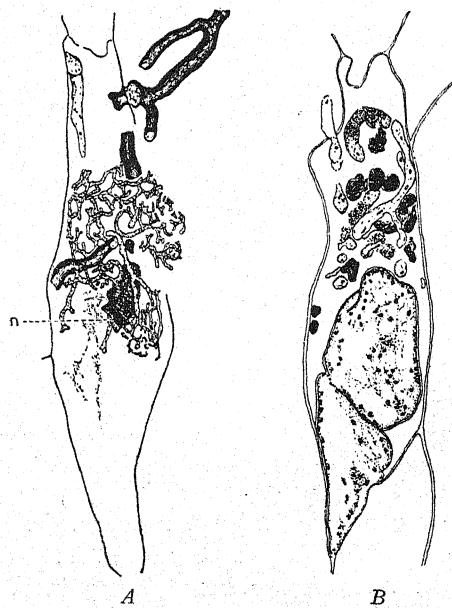


Fig. 57. A, *Pellia epiphylla*: arbuscule in a cell of the thallus. n, cell-nucleus. Original $\times 695$. Reduced about $\frac{1}{3}$. B, *Pellia epiphylla*: cell of the thallus enclosing two multinucleate vesicles. Original $\times 695$. Reduced about $\frac{1}{3}$. (From Magrou, *Ann. d. Sc. Nat.* 1925.)

deductions from experimental cultures. The success of aseptic spore cultures, whether upon sterilised soil or upon artificial media, was found to depend upon the existence in the substratum of a H-ion concentration corresponding to that of the soil upon which the parent plant had been growing in nature, viz. a *pH* value of about 4.85. Under such conditions, thalli in aseptic cultures showed rapid growth and uninterrupted apical development. By comparing plants so obtained with infected thalli, Magrou has inferred the existence of alternating phases of rest and differentiation determined by infection.

At the time of publication (one year from sowing), sexual organs had not been formed by the plants in these cultures¹.

It has been pointed out by Magrou that a causal relation may exist between the high degree of acidity found necessary in his aseptic cultures of *Pellia* and the absence of mycelium in the absorbing region of the thallus. It is clear that this condition is not invariably fulfilled in nature, e.g. his experimental plants were derived from members of a colony upon acid soil ($\text{pH} = 4.85$), whereas those used by Ridler were found growing upon soils the reaction of which was approximately neutral ($\text{pH} = 6.8$ to 7.0). If the endophytic mycelium plays any part in the regulation either of the osmotic equilibrium or of the H-ion concentration of the cell sap this discrepancy might be susceptible of explanation.

Recognition that the proximity of archegonia and young sporophytes constitutes a definite bar to the spread of mycelium in *Pellia* has helped to clear up confusion in the literature in respect to sporophyte infection in Liverworts. It had been stated by more than one of the earlier workers, including Gallaud, that fungal infection in Bryophyta is limited to the gametophyte. There then appeared a series of records of sporogonial infection—Leitgeb (1879) for *Ptilidium*, Cavers (1903) for *Lophocolea tridentata*, *Radula complanata*, *Cephalozia bicuspidata*, and *Plagiochila asplenoides*. Reviewing these observations in the light of his own researches, Cavers concluded that the relation in sporophyte infection was “simply that of parasitism.”

More recently Ridler (1922), working on *Pellia*, after recording that—“Normal healthy sporophytes were repeatedly examined, and no sign of the fungus was discovered in foot, seta or capsule”—observed subsequently that mycelium was present in certain abnormal capsules, and isolated a species of *Phoma* from the infected tissues. At the time of the observation, the account given implied identity of this mycelium with that present in the tissue of the thallus. It was concluded from the condition of the infected sporogonial tissues that the relationship was parasitic on the part of the fungus:—“The fungus causes a disease, killing the tissues of the sporogonium, and in some cases rendering them abortive.” Attempts to obtain experimental proof by inoculation into uninfected thalli

¹ Killian (1923-1924) has recorded the production of sporogonia by various members of the Jungermanniaceae in pure cultures. He attributed lack of success in the case of *Pellia* to the absence of the specific endophyte, and has undertaken further experiments with a view to securing further evidence on the subject.

were not attended by success, and it was admitted later that the confirmation of the identity of the two mycelia was lacking (Ridler, 1923). On general grounds there appears little reason to believe that they belong to fungi related in any way to one another. All the facts recorded and figured point to pathogenic infection of the sporophyte by a parasitic fungus, doubtless the species of *Phoma* isolated by Ridler. Viewed thus, the case falls into line with others recording sporophytic infection in Liverworts, and confirms rather than contradicts the theory of sporophytic immunity offered by Magrou.

As a transitional group from the thalloid to the foliose types, the Aneuraceae have a somewhat special interest. It was known that species of *Aneura*, e.g. *A. pinguis*, showed fungus infection of the rhizoids and neighbouring cells. Denis (1919) described a "biologic form" of *Aneura* sp. without chlorophyll although apparently healthy since normal sporogonia were produced on some of the fronds. These thalli showed profuse intracellular infection of the rhizoids and ventral tissues by an endophytic fungus which formed typical "pelotons" in the cells. The mycelium resembled that noted in *Aneura pinguis*, but the colourless thalli showed markedly heavier infection, held by Denis to be directly related to the absence of chlorophyll. No experimental data were obtained. An infection of similar type in a normal green species of *Aneura* is shown in the photograph reproduced in Fig. 58. In this case likewise the mycelium is similar in habit to that of the Orchid endophytes. It forms "pelotons" which are subject to digestion by the cells of the host. This kind of infection appears to be constant for *Aneura*, and is markedly different from that recorded in members of the Marchantiaceae and Jungermanniaceae, in which the endophytes belong to the familiar mycorrhizal type producing vesicles and arbuscules. In view of Peyrone's recent conclusions respecting the presence of two different endophytes in the mycorrhiza of Flowering Plants, this observation is noteworthy. Whether infection by both types of fungi can occur simultaneously in Liverworts is at present unknown.

In respect to fungus infection in the higher members of Bryophyta, endotrophic mycelium is well known to occur regularly in certain Moss genera, e.g. *Buxbaumia* and *Tetraphodon*. Peklo (1903) described it in the capsule of *Buxbaumia aphylla* and interpreted it as a case of "mycorrhizal association." Cooke (1889) and Britton (1911) recorded *Cladosporium epibryum* on various Mosses. Györffy (1911) noted the presence of *C. herbarum* on capsules of *Buxbaumia viridis*.

Schimper (1858) and subsequent workers had observed the presence of small "microspores" together with spores of normal size in capsules of *Sphagnum*; the former were regarded as "male spores" but were afterwards identified as the chlamydospores of a "Smut" fungus, *Tilletia sphagni* (Nawaschin, 1892).

In general, it may be concluded that there is practically no evidence at present for the existence of anything in the nature of a mutualistic relation with fungus mycelium in Mosses as a whole, while the claim for its existence in certain specialised genera, e.g. *Buxbaumia* and *Tetraplodon*, lacks experimental confirmation.

Pteridophyta.

In Vascular Cryptogams, fungus infection may involve either phase in the life history or affect both gametophyte and sporophyte generations. The word "mycorrhiza," to describe an association of fungus mycelium with the prothallus, is obviously a misnomer but, as in Bryophytes, its use has been sanctioned by custom. Since the biological relation is evidently similar and may even involve the same fungus in both generations, it is clear that any full account of the condition in Pteridophytes must include both phases.

Equisetales. It is curious that there is no record of mycorrhiza in the genus *Equisetum*, several species of which frequent soils rich in humus. In *Equisetum arvense* and similar forms, the deep-growing habit of the rhizomes may afford an explanation of its absence. The association of a reduced transpiring surface and other indications of xerophily with absence of fungus infection appeared to offer a direct challenge to the theory of infection put forward by Stahl, but an experimental enquiry by this observer permitted him to record the existence of a relatively rapid transpiration current in species of *Equisetum*.

The invasion of the prothallus of *Equisetum* by a species of *Pythium*, put on record by Sadebeck (1875), appears to have been merely an isolated case of ordinary parasitic attack.

Lycopodiales. In this group of Pteridophytes, most of the interest relating to fungus infection is centred in the gametophyte stage.

The prothallus of *Lycopodium* is still a botanical rarity, known to comparatively few botanists. This is not due to lack of interest in the genus, but to the two circumstances that the small, subterranean gametophytes are difficult to discover in nature and have only recently been collected in any abundance, while their cultivation from spores presents difficulties.

The history of attempted spore germination goes back to the end of the eighteenth century, when an English surgeon, John Lindsay (1794), reported successful germination of the spores of *Lycopodium cernuum*, but unfortunately left on record no details beyond the fact of "a vegetable growth taking place where they (the spores) were sown." Spring (1842) failed to secure germination and attributed his failure to the existence of male plants only! This was before Hofmeister (1851) had correctly predicted that spores of *Lycopodium* would produce—not leafy plants, as was generally assumed at the time—but prothalli bearing sexual organs. Hofmeister, unfortunately, failed to secure proof of this by means of spore germination. Some success was achieved by de Bary (1858) who germinated spores of *Lycopodium inundatum*, but was unable to maintain the young prothalli beyond a ten- or eleven-celled stage. Beck (1880) also germinated spores of this species with a similar result.

The first discovery of gametophytes in nature was made by Fankhouser (1873), who found four prothalli of *Lycopodium annotinum*, with sporelings attached. These, combined with the early stages of development previously observed by de Bary, provided a general idea of the structure of the gametophyte of *Lycopodium*. Large contributions to the knowledge of this still somewhat mysterious stage in the life history were then made by three or four botanists, of whom two, at least, carried out researches now classical in the history of the subject. Goebel (1887) found and described prothalli of *L. inundatum*, thus completing the story begun by de Bary nearly thirty years earlier.

In 1884 Treub (1884-1890) published the first of his elegant researches on tropical species of *Lycopodium*. In a series of papers entitled *Études sur les Lycopodiacees* he figured and described the development and structure of the gametophytes and young sporophytes of a number of species as found in nature, and recorded also the results of a series of laboratory cultures of the spores. These accounts have become a part of standard botanical literature and need not be recapitulated here. The prothalli described included partially subterranean cylindrical forms with chlorophyll in the upper region (*L. salakense*), similar forms with leaf-like green expansions at the surface (*L. cernuum*), tuberous forms without chlorophyll, entirely subterranean in habit (*L. clavatum*), and the colourless branched saprophytic forms belonging to *L. phlegmaria* and related epiphytic species. Treub germinated the spores of *L. cernuum* in the laboratory on soil brought from stations carrying the plant in

the field and, under these conditions, succeeded in growing the prothalli to a relatively advanced stage of development. They showed characteristic infection by an endophytic fungus, the mycelium occupying the cells of a median zone in the lower, colourless part of the prothalli.

Treub thus described infection in the prothallus of *L. cernuum*:—“Les cellules périphériques des tubercles renferment toutes les filaments d'un champignon endophyte appartenant probablement au genre *Pythium*.” The mycelium was found in all the prothalli examined, and was apparently harmless to the cells (Treub, 1885).

To Treub the most striking feature of infection was the distribution of the hyphae, intracellular in the peripheral regions, and strictly intercellular in the more centrally situated tissues. Subsequently, he described the gametophytes of a number of other species—*L. salakense*, *L. phlegmaria*, *L. hippuris*, and *L. nummularifolia*. *L. salakense* has a green aerial gametophyte. When sown, the spores germinate at once, and, in this species only, Treub succeeded without difficulty in raising mature prothalli with antheridia and archegonia. There is no mention of fungus infection in these prothalli, and Treub regarded them as holophytic in nutrition, although they lacked the green leaf-like expansions which crown those of *L. cernuum*:—“En effet, les prothalles de *L. salakense* ne vivent certainement pas en saprophytes; ils sont distinctement verts, bien qu'ils ne contiennent pas autant de chlorophylle que ceux de *L. cernuum*” (Treub, 1887-1888).

The gametophyte of *L. phlegmaria* is a branched structure without chlorophyll, bearing gemmae or bulbils which grow directly into new prothalli. The distribution of the endophytic fungus is entirely intracellular in this species. Those of *L. carinatum*, *L. hippuris* and *L. nummulariforme* are of similar habit. Treub failed to germinate the spores of these saprophytic forms. In the case of *L. phlegmaria*, he put on record his conviction that the relation with the endophyte was not parasitic:—“le champignon abrité par le prothalle pourrait payer le service rendu en contribuant à la nourriture de son hôte. Il y aurait mutualisme.”

While Treub's researches were in progress, Frank's papers on mycorrhiza appeared and his theory of beneficial symbiosis challenged attention. Treub, however, was hardly prepared to admit this relation for *Lycopodium* prothalli in general. In *L. cernuum* and *L. inundatum*, for example, he inclined to the view that the endophytes were harmless intruders—“de faire peu de mal” or “de ne

pas tuer les prothalles." With regard to the identity of the endophytes, he had originally referred that of *L. cernuum* to the genus *Pythium*. In view of his own later observations and those of Wahrlich (1887) on the root fungi of Orchids, he did not press this suggestion, nor did he put forward any subsequent views on the subject.

Simultaneously with Treub's work on the tropical species, Bruchmann's (1885-1898) patient and protracted investigations on north European species of *Lycopodium* revealed the full life history of those much more difficult forms with subterranean prothalli. Bruchmann (1885) found and described the gametophyte of *L. annotinum*, and, thirteen years later, those of *L. clavatum*, *L. complanatum*, and *L. selago*. After repeated efforts, he succeeded in germinating spores of several species, a remarkable feature being the extreme slowness of germination. For example, spores of *L. selago* began to germinate 3-5 years from sowing, while the mature prothallus took 6-8 years to develop; those of *L. clavatum* and *L. annotinum* were even slower, requiring from 12-15 years to reach sexual maturity. The gametophytes of all these species are small subterranean tuberous structures, destitute of chlorophyll, and apparently saprophytic in nutrition.

Bruchmann recorded and figured mycelium in the rhizoids and adjoining tissues, and observed invasion of the young prothallus at the four- or five-celled stage by an endophytic fungus. He suggested that it might be possible to shorten the protracted germination period by supplying a suitable stimulant, but did not carry out any experiments on this aspect of the subject.

Almost simultaneously with Bruchmann, Lang (1899) discovered and described the gametophyte of *L. clavatum*. The prothalli of this species are very small tuberous bodies, entirely subterranean, and destitute of chlorophyll. In the main, the distribution of infection is similar to that of the other saprophytic forms—an outer layer of cells apparently free from mycelium, a peripheral zone showing profuse intracellular infection, and a central region, with hyphae confined to the intercellular space system, produced by separation of adjacent cells along the middle lamellae. In the last-named region, the cells contained abundant starch and evidently constituted a storage tissue.

Lang described the mycelium as non-septate with multi-nucleate vesicles similar to those recorded by Janse. Arbuscules and sporangioles were not recorded, but the figures show cells containing hyphae contracted about the nuclei. The gametophyte of *L. clavatum*

was regarded as a "total saprophyte with a fungus found living as a symbiont in the tissues probably acting in some way as intermediary."

The variety of structure found in these gametophytes had led Bruchmann to suggest a classification of the genus based on the characters of the prothallia, but Lang's view, that the observed differences of structure were related to habitat and nutrition rather than to systematic affinities is now commonly accepted. These differences, for example, the green assimilating lobes of the gametophyte of *L. cernuum*, and the capacity to produce chlorophyll when exposed to light exhibited by those of *L. selago*, doubtless affect the mode of nutrition, but they have little influence upon fungus invasion, which occurs indifferently in all species.

During recent years, the gametophytes of a number of other species of *Lycopodium* have been discovered, and all agree in general structure with one or other of the types exemplified by *L. cernuum*, *L. phlegmaria*, and *L. clavatum*. Holloway (1920) and Chamberlain (1915) have described those of various New Zealand species. Discussing the profuse fungus infection in the median zone of the subterranean prothallus of *L. volubile*, Chamberlain observed that The foot of the sporophyte is strongly haustorial, and the cells surrounding it have some starch but very little protoplasm or other visible contents; consequently the food supply must come largely from the fungus region and must be in a liquid condition even at a considerable distance from the foot.

Spessard (1917) and Stokay and Starr (1924) have given accounts of thalli and sporelings of several American species, and Degenen (1924) has recorded the discovery of several hundred gametophytes of *L. obscurum* in a single station. The latter author has also recorded the presence of thousands of prothalli and young sporophytes of *L. cernuum* in volcanic crevices in Hawaii under conditions of abnormal heat. None of these recent observers has devoted special attention to the details of fungus infection.

Reviewing the somewhat scanty data derived from artificial culture of prothalli, it seems legitimate to conclude that, in general, the spores of those forms with green aerial prothalli germinate readily and are entirely or comparatively independent of fungus infection. Those of species with colourless saprophytic prothalli have either not germinated at all under artificial conditions, or have done so with extreme slowness. All the records point to a dependence of germination upon fungal invasion very similar to that in Orchids.

As might be expected from their size and subterranean habit, the prothalli of *Lycopodium* are not readily discovered in nature, and information as to the exact conditions required for their development is still relatively scanty. Ordinarily, they have been found growing sporadically in localised areas identified by the presence of young sporophytes. It may be hoped that recent discoveries on a relatively large scale may lead to fresh information bearing on the exact relation between development and fungus infection, and provide some indication of the specificity or otherwise of the endophytic fungi.

The sporophyte of *Lycopodium* has commonly been described as free from fungus infection and there is at present no record of the formation of ordinary mycorrhiza by any species. In view of the existence of what is probably an obligate relation in the gametophytic phase, the subject is of some interest, and there are observations of possible significance in the literature. Bruchmann (1874) investigated the anatomy of several species of *Lycopodium* without making any record of fungus infection, but in *L. inundatum* he described a tuberous development of the young stem, and the formation of a peculiar tissue—"Polstergewebe"—characterised by the separation of the cells, and the deposition of granular material between them. This tissue appears in the basal part of the young sporophyte and sporadically in the stems of the older plants, and Bruchmann believed that it functioned in relation to the storage of water. Kühn (1889) made similar observations on *L. inundatum*, noted the presence of fungus mycelium imbedded in the slimy material between the cells, and observed that the hyphae could become intracellular—"Das Polstergewebe von *Lycopodium inundatum* enthält ebenfalls eine Pilzinfection." Goebel (1887) likewise reported fungus infection in the sporophyte of this species of *Lycopodium*. Kühn believed that the production of intercellular slime was directly related to the presence of endophytic mycelium, but was uncertain as to its exact origin, whether from the cell walls or those of the hyphae. Treub (1889-1890), investigating the embryo and young plant of *L. cernuum*, observed the presence of mycelium similar to that in the prothallus—"La plantule du *Lycopodium cernuum* est habitée de même par un champignon, sans doute le même qui se trouve dans le prothalle." The tissue of the embryonic tubercle or protocorm in this species is differentiated into a central mass with large intercellular spaces and a parietal investing layer. At an early stage, the fungus penetrates these intercellular spaces; in older protocorms, the mycelium appears to fill all the free space between the cells and serves to accentuate

the contrast between the two kinds of tissue. The central cells retain their nuclei but do not possess starch which is present in the cells of the parietal layer. The young plants of *L. cernuum* produce root tubercles in which the constituent cells become rounded off, leaving intercellular spaces which also, at an early stage, undergo invasion by the mycelium of the endophyte.

The existence of a causal relation between infection and tubercle formation in this species of *Lycopodium* clearly requires investigation. Treub did not put forward any final views respecting the physiology of infection—"Il est hors de doute que l'endophage ne fait pas de mal aux plantules. Au contraire on reçoit l'impression qu'il y a un certain mutualisme entre le tubercle et le champignon."

To elucidate the exact nature of this relation, he pointed out, would require long and patient researches. In spite of Frank's views he evidently regarded the whole subject of the association of vascular plants with fungi other than parasites as still within the region of hypothesis. The rôle assigned by Frank to the root fungi of trees he accepted as possible for the saprophytic prothalli of *Lycopodium* spp., but improbable for the prothallus and young sporophyte of *L. cernuum*, since the latter prefers soils markedly deficient in humus.

With regard to other genera of the Lycopodiales, Bruchmann (1897) reported fungus infection in the roots of *Selaginella spinulosa*, while Stahl (1900) recorded it as absent from those of *S. helvetica*, correlating this observation with the abundant development of root hairs in the latter species. In the rhizome of *Psilotum triquetrum* mycorrhiza was recorded by Solms Laubach (1884), who also observed and figured invasion of the vegetative bulbils by a mycelium—"dont les branches commencent à former les pelotons des hyphes qui se trouvent toujours dans le tissu de la plante." It was noted also by Janse (1897), and by Bernatsky (1899), who attempted to isolate the endophyte and extracted a form which he regarded as a *Hypomyces*.

Later, Shibata (1902) undertook a cytological study of the mycorrhiza of *Psilotum* and described it in detail. He noted that the intracellular mycelium underwent complete disintegration by the digestive activity of the host cells and recognised a differentiation of the infected tissue to "Pilzwirthzellen" and "Verdauungzellen" similar to those of Orchids. The nuclei of infected cells showed signs of great activity, and were believed to directly influence both the digestion of mycelium and the production of an amyloid-like material in which the hyphal residues became imbedded. The intracellular mycelium was of the non-septate type and produced vesicles containing fatty substances.

A gametophyte believed to be that of *Psilotum* was described by Lang (1901). The prothallus was found embedded in humus in the neighbourhood of the sporophyte on the stem of a tree fern. It was a small tuberous body about a quarter of an inch in diameter, without chlorophyll, but developing a faint green colour in the exposed tissues. The external layer and the central tissues were free from mycelium; between them, a peripheral zone of cells showed profuse intracellular infection by fine mycelium with vesicles of the usual type, bounded internally by a layer of cells marked by a somewhat unusual development of intercellular vesicles.

The prothallus of *Tmesipteris*, described by Holloway (1917), and by Lawson (1917, 1918), is also a non-chlorophyllous saprophytic structure showing endotrophic fungal infection of the usual kind.

Ophioglossales.

The three genera belonging to this group are included in the single family Ophioglossaceae. In general, the sporophytic tissues are of simple type. The rather fleshy roots are unbranched or very sparingly branched, and are otherwise characterised by the complete absence of root hairs and the development of typical mycorrhiza in the middle region of the cortex. Russow (1872) recorded fungus infection in mature roots of *Ophioglossum vulgatum*. Bruchmann (1894) discovered it in *O. pendulum*, an observation confirmed later by Janse (1897) and Campbell (1907). Subsequently it was found in other species, notably in the remarkable reduced form *O. simplex* (Bower, 1904).

In transverse section, the roots of *Ophioglossum* show a broad parenchymatous cortex with a zone of typically infected cells towards the middle region.

In *Botrychium*, Grevillius (1875) recorded root infection in twelve species, Kühn (1889) described it in the Moonwort, *Botrychium lunaria*, and Bruchmann (1906) observed it in roots of young plants of the same species, noting that its presence at this stage associated with slow leaf development implied a saprophytic habit for the early stages of growth. Holle (1876) observed that the stronger roots of *Botrychium* were free from infection, which was confined to those showing diarch structure. Marcuse (1902), commenting on the mycorrhiza of *Botrychium lunaria*, remarked that it differed from those of most mycorrhizal plants in that the starch content of the infected cells showed no diminution after entry of the mycelium.

In *Helminthostachys*, Farmer (1899) recorded mycelium in the

first three or four roots of the sporophyte, and its absence from those which developed later.

It may be concluded, therefore, that endotrophic mycorrhiza occurs generally in all members of the Ophioglossaceae, but is somewhat inconstant in appearance. Up to the present, this inconstancy has been related to the age of the plant and to that of individual roots rather than to factors in the external environment.

The prothalli in all known members of the family are of the subterranean type familiar in *Lycopodium*. In certain species, traces of chlorophyll have been observed; otherwise they are small cylindrical or tuberous structures, subterranean in habit, quite destitute of chlorophyll, and showing extensive infection by an endophytic fungus. As in *Lycopodium*, knowledge of the gametophytes has been derived partly from prothalli found in nature, partly from artificial cultures. The first to be described, that of *Botrychium lunaria*, was found by Hofmeister (1854). Subsequently, those of various species of *Ophioglossum* were discovered by Mettenius (1856), Campbell (1895, 1907), Lang (1902) and Bruchmann (1904); those of *Botrychium* by Campbell (1893), Jeffrey (1895), Lyon (1905) and Bruchmann (1906); and that of *Helminthostachys zeylanica* by Lang (1902).

Campbell described the gametophytes of *Ophioglossum molucanum* as from 5 to 10 mm. long, Mettenius those of *O. pedunculosum* as varying from 1.5 lines to 2 inches in diameter. In all species they are usually thickened to form a tuberous swelling at the basal end, and exhibit extensive intracellular infection by mycelium in all but the apical regions. In that of *O. pendulum*, described by Lang (1902), the mycelium was noted as closely resembling that observed by Janse (1897) in roots of sporophytes of the same species. In the young prothallus, mycelium occupies the superficial cells at the base and extends into the central tissues of the lower half, avoiding the meristematic tissue and that bearing reproductive organs. The prothalli of *O. pendulum* were found growing in humus among the leaf bases of epiphytic ferns, and probably persist for several years. Infection is conspicuous and the mycelium suffers intracellular digestion. Spores of this species and of others germinate readily in artificial cultures, but have not been observed to develop beyond the 3-celled or 4-celled stages lacking infection. Following his own observations and experiments, Campbell observed—"It is pretty certain that the association with the fungus is a necessary condition for the further development of the endophyte."

The prothallus of *Botrychium* is infected in a similar manner.

Both in *B. virginianum* and in *B. lunaria*, infection extends throughout the greater part of the central tissue leaving a peripheral region, including the meristem on the upper side, free from infection. As in *Ophioglossum*, it probably takes place at an early stage of development (Campbell, 1911). It is reported that invasion by the endophyte is followed by disappearance of starch and accumulation of oil, the latter not readily soluble in alcohol.

The gametophyte of *Helminthostachys zeylanica* has been described by Lang (1902). As in the other genera, mycelium is invariably present showing a distribution similar to that in *Botrychium*. Attempts to germinate spores were unsuccessful, and it may be surmised that the presence of the endophyte is one of the factors essential to success.

The character of the mycelium found in the gametophyte is similar throughout the group. The intracellular hyphae are variable in size and in form, in some cells swelling out to sac-like vesicles, in others giving rise to spherical structures recalling the sexual organs of members of Peronosporaceae. From this similarity, Jeffrey (1898) concluded that the endophyte of *Botrychium* showed affinities with the genera *Pythium* and *Completozia*.

There is no mention of "arbuscules" or "sporangioles" in the literature, although the intracellular mycelium apparently undergoes digestion, and in other respects the endophyte resembles the ubiquitous "Phycomycete type" recorded by Peyronel. In respect both to the obligate character of the association in the gametophyte phase and the identity of mycelium in gametophyte and sporophyte generations more information derived from experimental cultures is required. From the known facts, it is reasonable to conclude that an obligate relation with specific endophytes has been evolved in the gametophytes of all genera, and that the young roots of developing sporophytes are subject to infection by the same fungus. Whether such infection is a necessary condition for the normal development of roots is not known.

Filicales.

In the Filicales, mycorrhiza formation in the sporophyte, and a corresponding type of fungus infection in the gametophyte, is found regularly in the family Marattiaceae and sporadically in other groups. It is of rare occurrence in the Leptosporangiate Ferns and has not hitherto been put on record for the Polypodiaceae (see p. 43).

Marattiaceae. For the six genera of ferns included in the Marattiaceae, there are a number of isolated records respecting root infection in the sporophyte, but practically no experimental data. Russow

(1872) summarised his comparative observations on members of this group and the Ophioglossaceae as follows:—

In den unterirdischen Wurzeln fallen die zwei bis drei inneren Lagen der Aussenrinde vor den übrigen in den Augen durch den Inhalt ihrer Zellen, der aus Zussammengeballten, schwach gelblich tingirten zum Theil durchscheinenden, zum Theil grümösen Massen besteht, die sich auf Zusatz von Jod dunkel schmutzig-gelb farben in den Wurzeln der Ophioglossen kommen in den entsprechenden Zellen ähnliche Conglomerate vor, die durch eingedrungene Pilzfäden vernascht zu sein scheinen; bei den Marattiacen waren keine Pilzfäden wahrzunehmen.

Kühn (1889) described endophytic mycelium in the roots of *Angiopteris evecta*, *Kaulfussia aesculifolia*, and *Marattia alata*, but sought in vain for evidence of infection in *M. fraxinea*. He claimed also to have isolated from roots of *M. alata* an endophyte which spored in pure culture. No proof of identity was obtained and, from the methods employed, it is not unlikely that the fungus in question was a member of the epiphytic flora of the roots. Stahl (1900) failed to observe infection either in *M. alata* or in *M. fraxinea*, but recorded it as constant in *Angiopteris evecta*. Gallaud (1905) figured the mycorrhiza of *Angiopteris durvilleana*, describing it as of similar type to that of *Arum maculatum* (cf. Fig. 12 a).

West (1917) published an account of his observations on a number of marattiaceous species, and his main conclusions are included in the following brief summary. In *Angiopteris henryi*, *Kaulfussia aesculifolia*, and *Marattia cooperi*, the endophyte was found regularly in the primary roots and earlier adventitious roots but was inconstant in appearance in those formed later. It was usually absent from the aerial parts of the roots, from a proportion of the mature roots of all species, and from all the roots of some of the plants examined. This inconstancy may explain the failure of Kühn and Stahl to find infection in certain species of *Marattia* and in *Danaea alata*, and also the statements made by Campbell (1900) and Charles (1911) respecting the distribution of the endophyte in older roots. There is no evidence that the incidence of infection is correlated in any way with soil conditions.

The distribution of mycelium is inter- and intracellular; vesicles and arbuscules are formed (cf. Gallaud, Figs. 13, 34, 35), the latter showing every stage of degeneration due to the digestive activity of the root cells. An unusual feature recorded by West is the presence of thick-walled resting spores believed to be identical with those

observed by Kühn in roots of *Kaulfussia*. Attempts to isolate the fungus met with no success. On the morphological characters, West believed its affinities were with members of Peronosporaceae, and he placed it in a new genus *Stigeosporium*, naming it, by reason of the habitat, *S. marattiacearum*.

The roots of *Danaea alata* and *D. nodosa* also form mycorrhiza, the endophyte being apparently not *Stigeosporium* but a distinct form. In view of the absence of reproductive bodies no attempt was made to determine the affinities and systematic position of these fungi.

The gametophytes of members of Marattiaceae are green thalli resembling those of the Leptosporangiate Ferns but more massive in structure and longer lived. Campbell (1911) recorded an endophyte similar to that found in the prothalli of members of Ophioglossales as present in almost every case in those of *Angiopteris evecta* and *Kaulfussia aesculifolia*. A similar fungus was known to occur in *Marattia douglasi* and was presumably also present in prothalli of other species of this genus.

In the central tissues, intracellular infection was observed to be associated with the disappearance of starch and degeneration of plastids in uninfected cells. The irregular vesicular swellings which suffer digestion in the prothalli of Ophioglossaceae are said to be absent. Experimental data are scanty but there appears to be no evidence that spore development is in any way bound up with infection.

In both groups of Eusporangiate Ferns, the biologic relations appear to be of the usual kind. In its mode of entry the endophyte behaves as a parasite, but the invaded cells show no symptoms of injury and the attack is confined to the absorption of starch and other non-living cell constituents, a proportion of which become once more available to the host by subsequent digestion of intracellular mycelium. There is, at present, no experimental data bearing on the possibility of nitrogen fixation by the endophytes, nor any which throws light upon their reaction to the organic constituents of the humus soils in which many of these prothalli grow.

Stahl (1900) drew a comparison between the Ophioglossaceae with their reduced root systems, absence of root hairs and regular endophytic infection and the Marattiaceae with—as he believed—a more efficient water economy and less frequent infection. In respect to the latter group he held that they occupied a position intermediate between the regularly infected Ophioglossaceae and the ordinary Ferns (Polypodiaceae) which were reported free from mycorrhiza.

Filices.

In this group—the Ferns in the popular sense—the formation of mycorrhiza is an uncommon phenomenon, a curious and at present unexplained fact in view of the distribution of the members on woodland and other humus-rich soils.

Janse (1897) observed root infection in *Cyathea* sp. in Java but found none in the epiphytic *Asplenium nidus-avis*. Stahl (1900) noted the absence of mycorrhiza from *Osmunda regalis*, the Hydropterids, and many members of Polypodiaceae; namely, *Aspidium filix-mas*, *A. lobatum*, *Asplenium filix-femina*, *A. viride*, *Pteridium aquilinum* and *Polypodium vulgare*. Frank (1887) had already observed that *Aspidium thelypteris* was uninfected. In view of the absence of any positive record of mycorrhiza in members of Polypodiaceae and the existence of more than one negative observation for *Aspidium filix-mas*, it is of interest to place on record its appearance in roots of this fern from the neighbourhood of London. In this, at present, unique record of mycorrhiza formation in the family Polypodiaceae, the mycelium is concentrated in a single layer of cells in the inner cortex and the intracellular mycelium shows the usual characteristic features. The relation is evidently entirely different from that in ordinary parasitic invasion by mycelium and shows the characters and features invariably associated with endotrophic mycorrhiza (Figs. 59, 60).

It is probable that endophytic mycorrhiza occurs in the roots of members of Polypodiaceae more commonly than has been supposed. I am indebted to Dr E. McLennan for the following unpublished note recording its occurrence in Bracken (*Pteridium aquilinum*):—

Roots of the Bracken fern (*Pteridium aquilinum*), obtained from Castlemaine, Victoria, Australia, when sectioned and examined microscopically, showed a typical endophytic mycorrhiza. It was noticed that entrance to the root was effected through the root hair, the travelling hyphae carrying the 'infection' horizontally through the outer and middle cortex, while the digestive zone occurred only in the endo-cortex. Arbuscules and sporangioles were observed in the two or three cortical cell-layers immediately adjacent to the endodermis. The soil from which the roots were collected was a heavy clay.

In the gametophyte generation of the Leptosporangiate Ferns, there are isolated records of infection, but no evidence of the existence of a specialised relation with the endophyte. In *Osmunda cinnamomea*, Campbell (1908) noted that many prothalli contained an

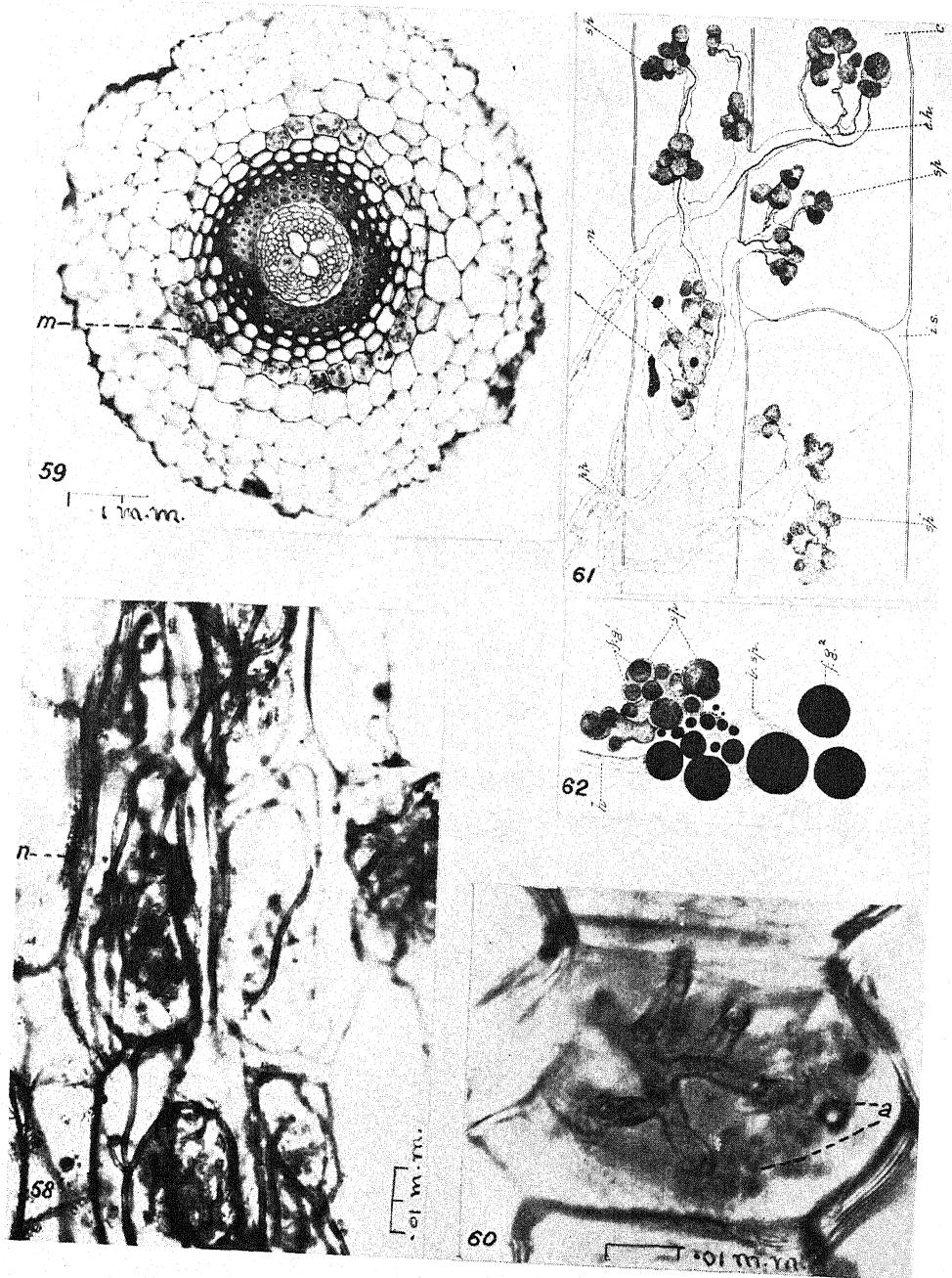
endophytic fungus resembling that in *Ophioglossum* and *Botrychium*. He also observed a similar type of infection in prothalli of four species of *Gleichenia* from widely separated geographical regions, namely, *G. polypodioides*, *G. dichotoma*, *G. laevigata* and *G. pectinata*. He concluded—"that an endophytic fungus is normally present in the green prothallia of several Marattiaceae, Osmundaceae, and Gleicheniaceae, and it is highly probable that further research will show similar fungal endophytes occurring in the prothallia of many other ferns." Campbell also put forward the view that the presence of the endophyte may have been an important factor in the evolution of the saprophytic, subterranean gametophytes of the Ophioglossaceae from green holophytic forms resembling those of Marattiaceae.

Commenting on the evidence of infection in Fern prothalli in general, Campbell has noted the possible occurrence of a series leading from complete saprophytism and dependence upon infection, as in Ophioglossaceae, to a more or less casual type of infection, as in the green prothalli of Marattiaceae and the families of Leptosporangiate Ferns.

With the exception of a few experimental observations on the germination of spores with and without the endophyte, there is at present no experimental evidence upon which to base an opinion as to the precise significance of infection in Ferns. There is evidently a close parallelism with the condition in Lycopods, both in respect to the inconstancy of infection in the sporophytes and its invariable association with a non-green saprophytic gametophyte stage.

The evidence put forward by Stahl (1900) in support of his theory of nutrition in mycotrophic plants has been subjected to criticism in more than one instance in the present review. His attempt to correlate fungus infection with economy of water exchange in Ferns was criticised by Bower (1908), who pointed out that there is less evidence of this in *Cyathea*, which forms mycorrhiza, than in *Asplenium nidus-avis* and *Osmunda regalis* which do not. Bower finds little evidence among Ferns that the mycorrhizal habit is an effective source of organic nutrient supply. If it were, he adds, it might be expected that examples would occur showing vegetative reduction and loss of chlorophyll, whereas, with rare exceptions, e.g. *Ophioglossum simplex*, this is not the case.

In Bower's opinion, the facts do not bear out the general assumption that mycorrhizal symbiosis, as seen in certain Pteridophytes, is directly associated with vegetative reduction of the infected sporophyte as a whole. In this respect the section of *Ophioglossum* known



RAYNER—MYCORRHIZA

as *Ophiiderma* is exceptional, and is regarded as providing a series in which mycorrhiza has become effective as a partial substitute for chlorophyll nutrition, while reduction of the vegetative system has actually followed as a consequence. *Ophioglossum simplex* represents an extreme case showing complete disappearance of the sterile lamina of the leaf.

The family Psilotaceae has also been cited as one in which a tendency towards reduction of the vegetative organs points to the efficiency of mycorrhiza as a nutritive mechanism.

EXPLANATION OF PLATE I

Fig. 58. *Aneura* sp. Cells of thallus showing infection by a mycorrhizal fungus of the *Rhizoctonia* (Orchid) type. *n*, cell nucleus.

Fig. 59. *Aspidium filix-mas*. Transverse section of root showing development to mycorrhiza. *m*, infected cells.

Fig. 60. Single cell from mycorrhizal layer shown in Fig. 59, more highly magnified. Main branches of intracellular mycelium with arbuscules, subsequent to digestion. *a*, arbuscules.

Fig. 61. *Lolium temulentum*. Cells from the innermost zone of the root cortex, prior to bursting of the sporangioles. At this stage, the cell contents include the nucleus, cell cytoplasm, shrivelled hyphae, and intact sporangioles enclosing the fat about to be liberated into the cell lumen. *n*, nucleus; *pp*, protoplasm; *i.s.*, intercellular space; *e.h.*, empty hyphae; *sp*, sporangioles; *c*, cell of the innermost zone of the cortex. Original $\times 1050$. (From McLennan, *Annals of Bot.* 1926.)

Fig. 62. Portion of a cell similar to those shown in Fig. 61 at the exchange stage, showing intact and burst sporangioles. *h*, hypha; *sp.*, intact sporangiole; *b.sp.*, burst sporangiole; *f.g.²*, free fat globules; *f.g.¹*, fat globules seen through wall of intact sporangiole. Original $\times 1260$.

(For text reference to Figs. 61 and 62, see Chapter XI.)

(To be continued)

THE SEEDLING DEVELOPMENT OF *FESTUCA RUBRA* L. VAR. *TENUIFOLIA* MIHI, AND ITS BEARING ON THE MORPHOLOGY OF THE GRASS EMBRYO

By W. O. HOWARTH, M.Sc., F.L.S.

(With 13 figures in the text.)

THE development of the grass seedling from the embryo during germination has already been much investigated. For the literature on this subject, and a consideration of the problems of morphology which it raises, reference must be made to the papers of Sargent and Arber (5) and Worsdell (6). The former, in classifying their types, regard that of *Avena* as the simplest. In my own investigations of the species of *Festuca* I have discovered a seedling development which appears to me to be still more simple, and which throws further light on the morphological nature of the parts of the grass embryo.

In germination the plumule grows up between the persistent glumes and is carried up upon a mesocotyl varying from 4 mm. to 1 cm. in length. Shortly after the commencement of germination two bulges can be seen at the cotyledonary node lateral to the insertion of the caryopsis (Fig. 1 a, 23 days old). Simultaneously with the elongation of the mesocotyl these grow out into the first two adventitious roots (Fig. 1 b, 36 days old). About this time three or four other roots appear at the base of the mesocotyl, and are followed by further roots from the base of the shoot as more leaves develop (Fig. 1 c, 41 days old). Externally, therefore, the seedling appears to conform to the *Avena* type described by Sargent and Arber, which has three "cauline" roots inserted at the base of the mesocotyl in addition to the "nodal" roots at the base of the shoot. But anatomical investigation shows that in *Festuca* all the roots are "nodal."

Development has been followed anatomically from the earliest stages of germination. The mature embryo, although extremely small, has its parts well defined (Fig. 2 a). The primordia of the vascular strands are here represented by shading in the scutellum and axis. The coleoptile bundles are shown as procambial strands in Fig. 2 b, which is slightly tangential of an embryo shortly after germination has commenced. They arise in a plane at right-angles

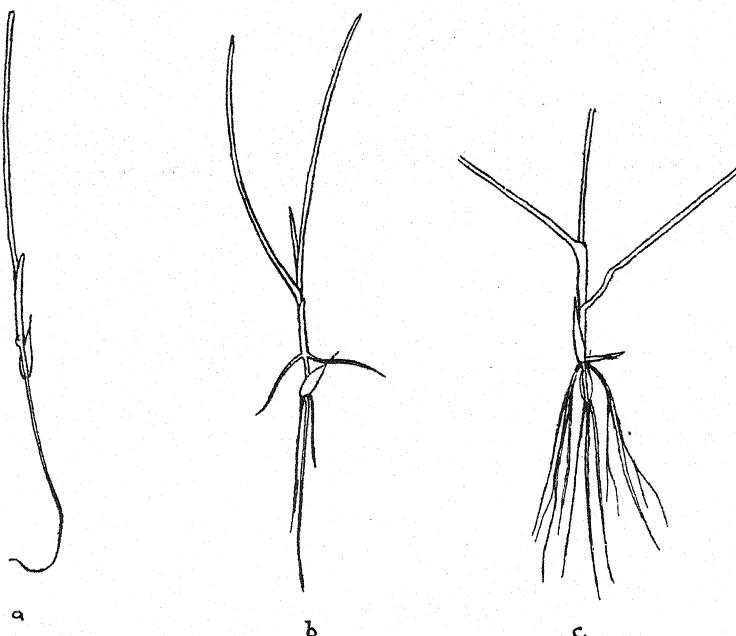


Fig. 1. Seedlings (a) 23 days old, (b) 36 days, (c) 41 days old. $\times 1\frac{1}{2}$.

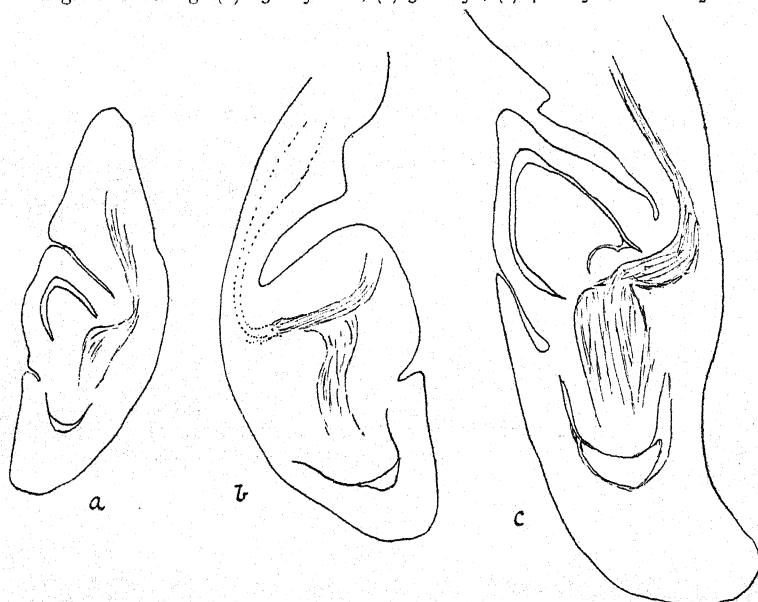


Fig. 2. Embryos before and soon after germination. $\times 80$. (a) Longitudinal section of ungerminated caryopsis. (b) Tangential longitudinal section, germinated a few days, showing junction of coleoptile trace with that of scutellum. (c) Longitudinal section, development of plumule.

to the section, at first gradually converge and then suddenly join the scutellum trace in the transverse plane just before it enters the axial stele and at a tangent to the latter. On the other hand, the median bundle of the first green leaf of the plumule enters the axial stele on the opposite side and quite distinct from the combined

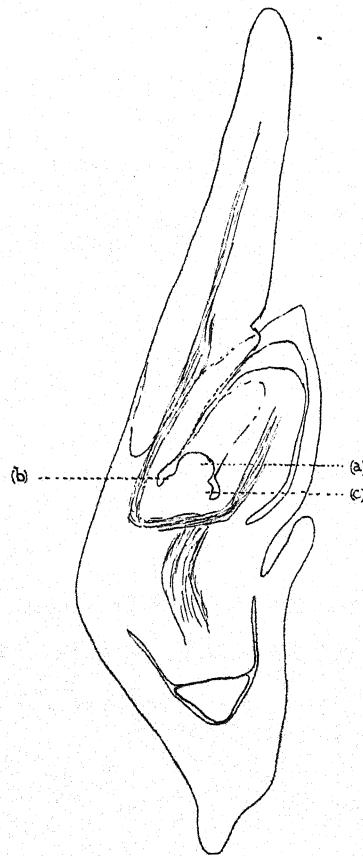


Fig. 3

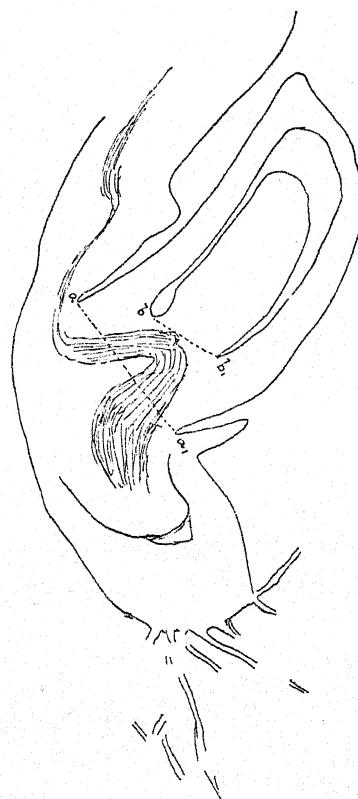


Fig. 4

Fig. 3. Longitudinal section of embryo, further development of plumule. $\times 80$.
 Fig. 4. Longitudinal section of embryo, commencement of formation of mesocotyl. $\times 80$.

scutellum and coleoptile traces (Fig. 3). In Fig. 3 the apical meristem is shown to be three-lobed. I interpret these lobes (a) the central, as the continuation of the shoot from which the second green leaf will develop, (b) on the left of (a), as an axillary bud on the same side as the scutellum and in its median plane, (c) on the right of (a) as

a similar bud axillary to the first green leaf. The bud (c) has grown out extravaginally in Fig. 1 c, but I have no evidence of (b) ever growing out. Percival (4) has found a similar bud in wheat which does develop into a branch in a small percentage of cases. He regards it as axillary to the coleoptile which he interprets as the third leaf of the axis, and makes the scutellum the first, and the epiblast the second leaves to fit in with his theory, but there seems to be no justification on anatomical evidence for thus far separating the

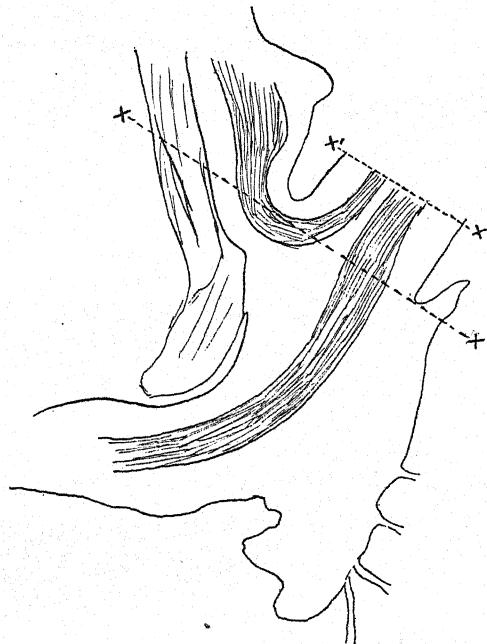


Fig. 5. Young seedling. Longitudinal section through attachment of caryopsis, coleorhiza with remnants of hairs, scutellum trace turning up mesocotyl, axial stele passing into primary root. $\times 80$.

scutellum and coleoptile. Along with Arber and Sargent and also Worsdell, I interpret them as parts of one and the same structure, the single cotyledon, and the bud as axillary to this. The first green leaf is thus the second leaf of the axis, and the two-ranked symmetry of the shoot laid down at once.

During this development the embryo is increasing in size. The scutellum extends so as to maintain contact with the gradually shrinking endosperm, and the coleoptile and coleorhiza enlarge. In all these organs growth is mainly due to the vacuolation of existing

cells, and this is how the mesocotyl comes into existence and grows. A comparison of Figs. 2 c, 3 and 4 shows its inception in the zone of tissue between the external (Fig. 4, $a \dots a_1$) and internal ($b \dots b_1$) faces of the coleoptile. By the longitudinal extension of this cylinder of tissue the scutellum trace is caused to turn upwards and to run parallel to the axial stele. Fig. 5 is a longitudinal section showing the bending round and upwards of the scutellum trace into the mesocotyl. Fig. 6 is a transverse section in the region of the bend of the scutellum trace (Fig. 5, line $x \dots x$) and also shows the axial stele in

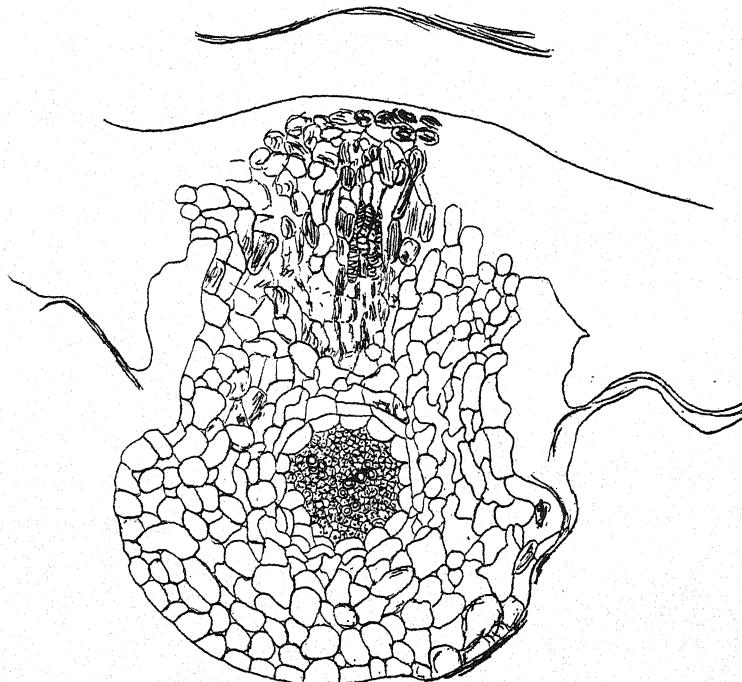


Fig. 6. Transverse section of young mesocotyl, line $x \dots x$ in Fig. 5. $\times 177$.

transition between mesocotyl and root. Fig. 7 is a transverse section across the mesocotyl (Fig. 5, line $x' \dots x'$) showing the scutellum trace as an inverted bundle with its phloem towards the mesocotylar stele. This condition has been well described by Sargent and Arber. Tracing the inception and development of the mesocotyl in this way it appears to be just to conclude that it represents the elongation of the cotyledonary node, or at least the upper portion of it. This conclusion fits exactly with that of Worsdell ((6), p. 522). The name mesocotyl for this structure is therefore singularly appropriate.

With the emergence of the coleorhiza into the soil "root-hairs" are produced from its superficial cells. This is no new feature, however, as Haberlandt⁽²⁾ quotes Schwartz as having observed them in *Panicum miliaceum* and *Setaria italica*, whilst he himself observed them in *Briza minor* and suggests that they are somewhat prevalent among grasses. Nishimura⁽³⁾ records them for *Poa pratensis* and *Phleum pratense*, and remarks that the epiblast may develop them also. In this connection he draws attention to Haberlandt's remarkable resemblance of the scutellar epithelial cells to root-hairs. The water requirements of the embryo are apparently supplied by the coleorhizal hairs, which remain capable of functioning for about 20 days in *Festuca* and about 30 days in *Poa*, *Phleum* and *Setaria* above. This practically covers the period during which the scutellum,

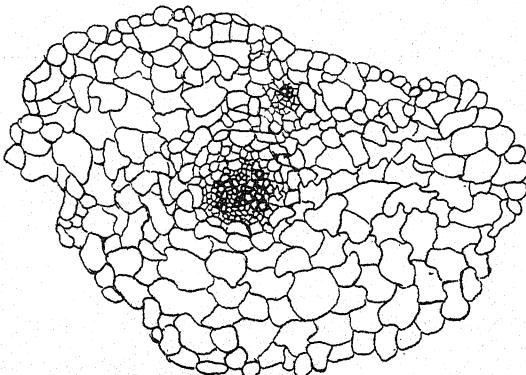


Fig. 7. Transverse section of young mesocotyl, line $x' \dots x'$ in Fig. 5. $\times 177$.

mesocotyl and coleoptile are functioning so that they would appear to be independent of the primary root, but certainly the scutellum must be, so that I am unable to agree with Sargent and Arber who explain the "xylem arch" between the scutellum trace and the mesocotyl as necessary in order to supply the scutellum with water from the primary root *via* the mesocotyl. It is a long way round, and the scutellum is already in contact with soil-moisture through the free surface of the embryo, and especially the coleorhiza. The xylem arch must be regarded as the normal, direct continuation of the scutellum trace into the axial stele. This is shown to be the case in *Festuca* by taking serial transverse sections through the upper region of the mesocotyl. In a young seedling, where other complications have not yet arisen, Fig. 8 shows the structure of the scutellum (left) and mesocotyl (right) bundles just below the point where the former turns

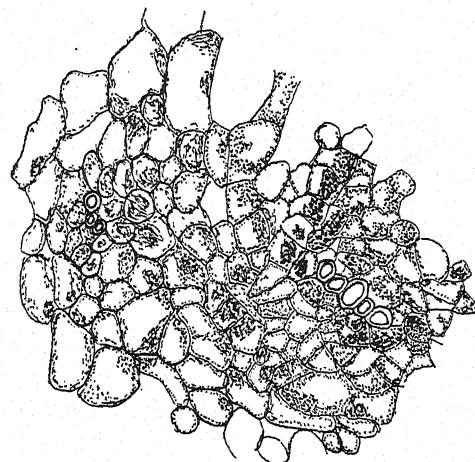


Fig. 8. Transverse section near apex of young mesocotyl, scutellum trace and mesocotyl stele. $\times 400$.

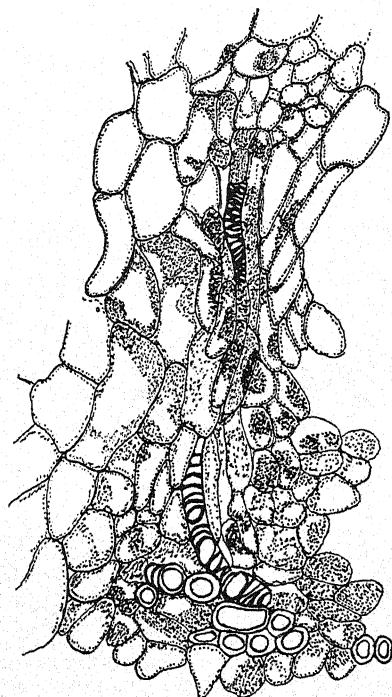


Fig. 9. Transverse section of apex of young mesocotyl just above Fig. 8, a coleoptile trace fusing with scutellum trace as the latter turns inwards into the mesocotyl stele. $\times 400$.

over into the latter. In Fig. 9 is seen the actual bending in of the scutellum trace. At the same time it is joined by one of the two coleoptile traces, the other having joined from below. There is no division of the coleoptile traces, they both pass in at right angles to the scutellum trace and in fusing with it turn slightly inwards

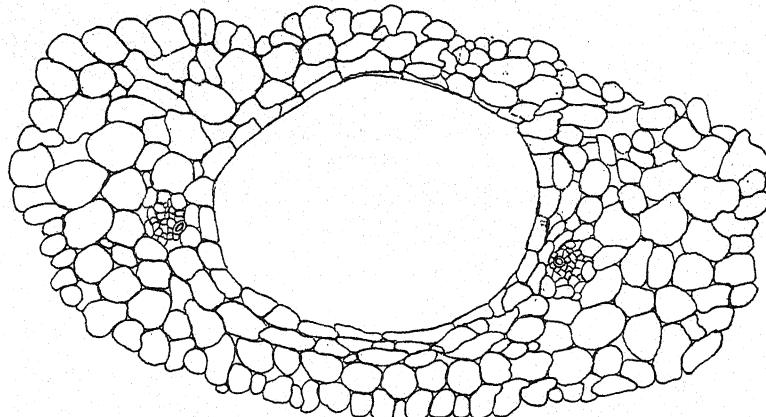


Fig. 10. Transverse section of coleoptile of young seedling. $\times 177$.

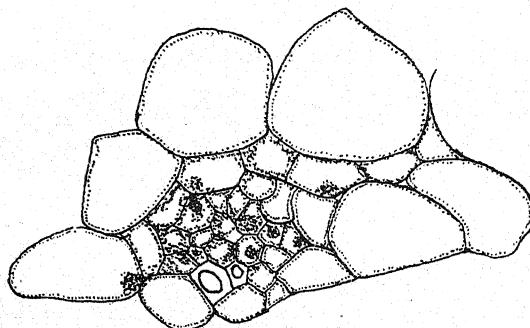


Fig. 11. Transverse section of a vascular bundle of the coleoptile. $\times 1400$.

towards the mesocotyl. The xylem on the right is that of the mid-rib of the first green leaf. Neither is there any evidence of doubling in the bundles of the scutellum and coleoptile, except, perhaps, in that whilst the xylem is poorly developed the phloem is strongly developed. Fig. 10 represents a transverse section of the coleoptile with its two vascular bundles one of which is shown enlarged in Fig. 11.

In reading through the literature treating with the vascular anatomy of monocotyledonous seedlings I have found the case of one which bears a striking resemblance to *Festuca*. This is the normal seedling of *Agapanthus* described by Coulter and Land (1). Reference to their Plate XXVIII, fig. 14, shows the cotyledon to have a median and two lateral bundles, and it will be seen that these compare with the scutellum and coleoptile bundles of *Festuca* in the way they join up just before passing into the axial stele. There is no mesocotyl in *Agapanthus*, but the axial stele becomes tetrarch in the primary root, and the protoxylem poles are set diagonally to the insertion of the cotyledon. This is precisely the case in *Festuca*. Further, the median bundle of the first green leaf of *Agapanthus* joins the axial stele opposite that of the cotyledon as in *Festuca*. In face of these facts I cannot help comparing the scutellum and coleoptile bundles of *Festuca* to the median and two lateral bundles of the one structure, a cotyledon, and in further support to point out that the first and successive green leaves of the seedling plant for some time have only three, a median and two lateral, bundles. As the seedling becomes more vigorous leaves with five vascular bundles are produced.

For the further description of seedling development I propose to take a single but representative example. The mesocotyl is still elongating, the shoot unfolding and adventitious roots forming. At the node of the first green leaf (the second node of the axis according to my argument) one adventitious root arises medianly, just under the insertion of the axillary bud, at the next node (the third) there are two, one median and the other lateral. But the roots from these two nodes do not emerge directly as do the pair from the first node, they elongate vertically and growing down through the cortex of the still elongating mesocotyl emerge from near its base, just above the epiblast and around the base of the primary root, as though they were "cauline" roots. A transverse section of one of these older mesocotyls is shown in Fig. 12. The epidermis is still more or less intact but the cortex is somewhat broken down, and in it are embedded two of the roots from above, each with tetrarch xylem. In the seedling from which this section was taken the mesocotyl had attained its maximum length. The stele is surrounded with a well-defined endodermis and there are two plates of metaxylem with protoxylem between. Above, on to these two xylem plates are inserted the first pair of adventitious roots and the two lateral bundles of the first green leaf. Indeed, the whole of the xylem system of the successive leaves and roots of the seedling shoot forms a connection

with them. The developing shoot is therefore able to draw its water from the nodal roots from an age of about 30 days. In Fig. 13 I have attempted to build up from serial transverse sections a transparent

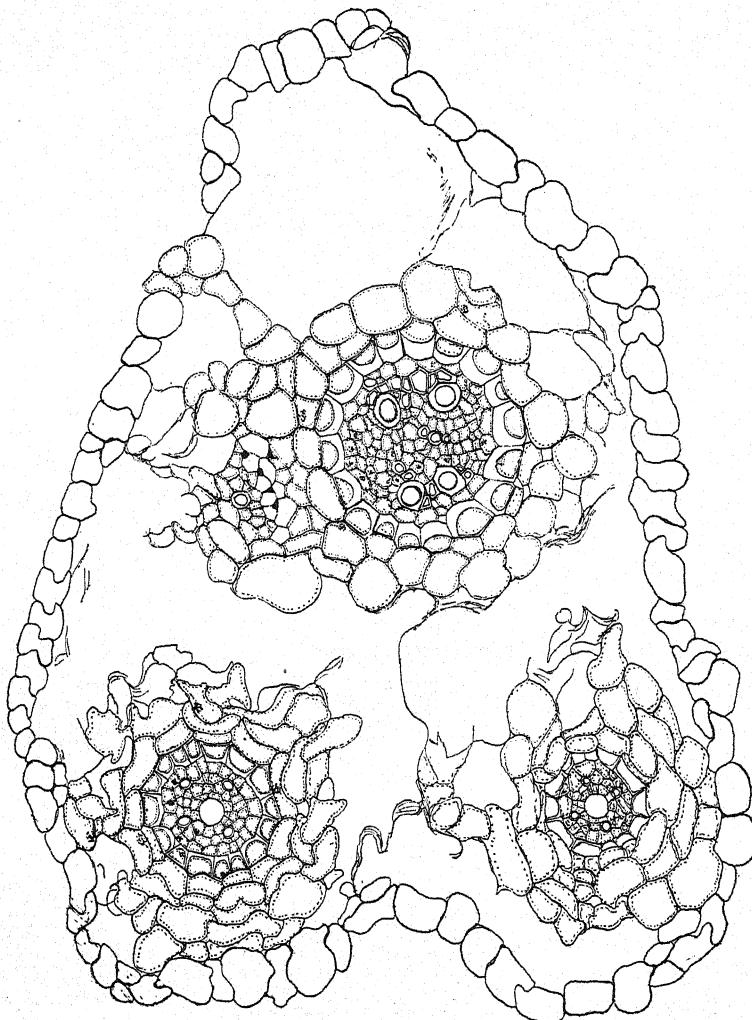


Fig. 12. Transverse section of mesocotyl of an older seedling containing two adventitious roots from base of shoot. $\times 266$.

model of the mesocotyl, including the bases of the shoot and primary root. The parts are not in proportion, the mesocotyl itself is much shortened and the parts above and below it greatly attenuated.

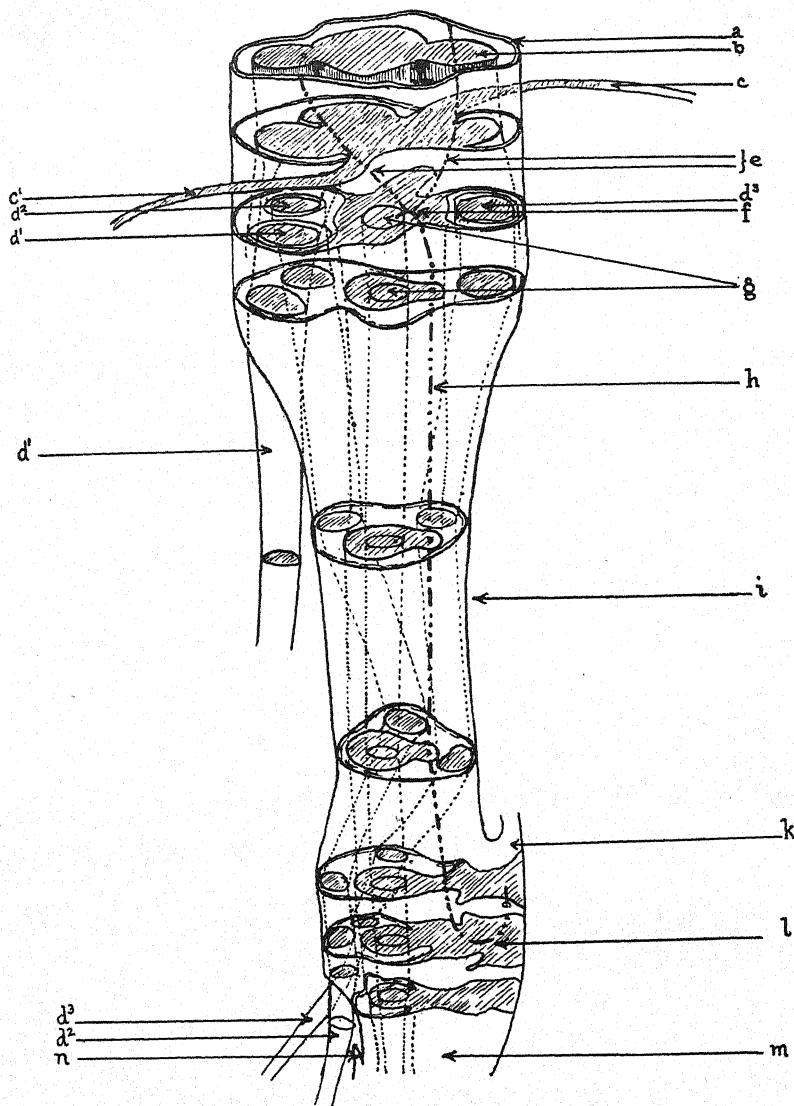


Fig. 13. Transparent model of mesocotyl (abbreviated), base of shoot and primary root (attenuated), built up from serial transverse sections.

a, coleoptile sheath; *b*, base of plumule; *c*, *c'*, first pair of adventitious roots; *d'*, *d²*, *d³*, three adventitious roots from the base of the plumule, of which *d'* emerges from the mesocotyl in the upper portion, while *d²* and *d³* growing down through the cortex emerge at its base just above the epiblast (*n*); *e*, coleoptile traces; *f*, junction of coleoptile traces with scutellum trace as the latter turns into axial stele (*g*); *g*, axial stele of mesocotyl; *h*, scutellum trace; *i*, mesocotyl, at this point with two adventitious roots *d²* and *d³* in its cortex; *k*, scutellum; *l*, point where scutellum trace (*h*) turns up into mesocotyl; *m*, coleorhiza enclosing primary root.

SUMMARY.

(1) The seedling development of *Festuca* presents a structure more simple than that found in *Avena* by Sargent and Arber

(2) It yields further support to the view that the coleoptile and scutellum are parts of one structure, a cotyledon

(a) from developmental evidence,

(b) from vascular anatomy.

(3) The mesocotyl represents the elongated cotyledonary node, or the major portion of it; thus supporting Worsdell's view.

(4) The growth of the mesocotyl during germination, and also of the scutellum, coleoptile and coleorhiza, is due mainly to the vacuolation of their cells.

(5) The "root-hairs" of the coleorhiza serve to supply water to and are probably sufficient for the needs of the scutellum during germination. The direct connection of the scutellum trace with the mesocotyl stele must be regarded as normal, and not, as Sargent and Arber suggest, absolutely necessary for the supply of water to the scutellum.

(6) The vascular anatomy of the seedling of *Festuca* is compared with that of *Agapanthus*:

(a) the scutellum and coleoptile traces with the median and two lateral bundles of the cotyledon,

(b) their entry into the axial stele opposite that of the second leaf, and the transition to tetrarch primary root, is the same in both cases.

(7) The adventitious roots which externally appear to be "cauline" at the base of the mesocotyl are really "nodal," but grow down through the cortex of the mesocotyl and emerge at its base.

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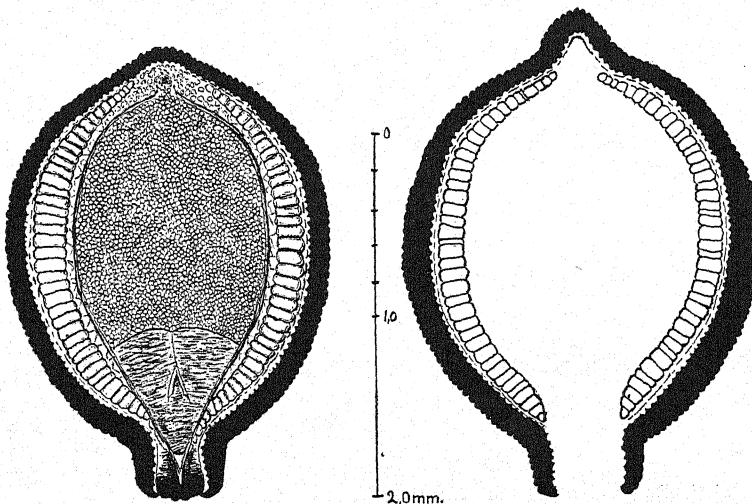
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INTERGLACIAL OCCURRENCE OF
ALDROVANDA VESICULOSA L.

By P. A. NIKITIN

(With 2 figures in the text.)

FINE black seeds, with a surface shining like metal, have been found by A. Nehring (1892, Klinge(1)), W. Szafer (1925, Samostrzelniki(2)), W. Dokturowsky (1923, Galitzch(3)), and myself (1924, Yaman, Gov. Voronezh(4)) in corresponding interglacial deposits.



Left, median longitudinal section of a recent seed of *Aldrovanda vesiculosa* L.
 After Korschinsky (6).

Right, median longitudinal section drawn to the same scale of a fossil seed
 now attributed to the same species. Original.

Probably these are the same seeds which were considered by Keilchak (from Klinge(5)) and E. Reid (from Galitzch(2)) as those of *Hydrocharis morsus-ranae* L. In fact, however, they are the seeds of *Aldrovanda vesiculosa* L. The seeds of this plant were characterised by S. Korschinsky(6) as follows: Seeds about 1.5 mm. long and 1 mm. broad, or somewhat larger, of broad elliptical form, at the micropylar end like a short-necked flask, at the opposite end slightly pointed. Surface pitch-black and shagreened (*laevis* of L. Diels(7) = *glaber*, but

not smooth). The outer rigid seed-coat of the fossil and recent seeds of *A. vesiculosa* remains apparently unaltered in boiling KOH and in a mixture of H_2SO_4 and $K_2Cr_2O_7$.

The accompanying figures illustrate the structure of the recent and fossil plant, and it will be seen that they match very closely.

Aldrovanda vesiculosa now inhabits (sporadically) Central and Southern Europe, Japan, India, Africa and Australia(7). Like *Trapa natans* L., *Nelumbo nucifera* Gärtn., *Salvinia natans* L. and certain other species, it is to be regarded as a relict, which is dying out. The same plant was found by me in interglacial lignite (Yaman) accompanied by *Salvinia*, *Brasenia*, etc. Up to now *Aldrovanda vesiculosa* L. has not been established in the fossil state.

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REVIEWS

A Monograph of the British Lichens. A Descriptive Catalogue of the Species in the Department of Botany, British Museum, Part II, 2nd edition, revised, by ANNIE LORRAIN SMITH, F.L.S. 8vo. Pp. viii and 447, with 63 full-page plates and one text-figure. Trustees of the British Museum, 1926. Price 20s.

This work is not merely a reprint of the first edition though the author, in the preface, states that "there have been no fundamental changes." The fifteen years which have elapsed since the publication of the first edition have brought forward new ideas as to the classification and arrangement of lichens and some of these have been adopted in the revised edition. *Dirina* and *Roccella* are placed amongst the *Graphidinae* whilst *Pyrenidium* and *Sarcopyrenia* find homes with the *Pyrenocarpeae*. More than a dozen species or varieties (*Gyalecia exanthemata* v. *dolichospora*, *G. cupularis* v. *marmorea*, *Lecidea prasinolepis*, *L. bauschiana*, *Biatorella pinicola*, *Bilimbia cambrica*, *Buellia canescens* v. *erubescens*, *Rhizocarpon roridulum*, *R. rubescens*, *Verrucaria microspora* v. *mucosula*, *V. microsporoides*, *V. muralis* v. *submuralis*, *V. rupestris* v. *ruderum*, *Staurothelia ebborensis*, *Arthopyrenia lomnitzenensis*, *A. gyalectoidea*, *Porina globosa*, *Clathroporina calcarea*) are included for the first time in this series of monographs whilst more than twenty-five additions to the British lichen-flora, which had been previously given in the appendix to the second edition of Part I, are placed in their proper positions. The careful revision of the arrangement of species, the painstaking addition of further localities and the insertion of the names of varieties and forms in the index show how great was the enthusiasm which enabled the author to accomplish such an arduous task.

The genus *Clathroporina* is new to the British Isles and, as the plates had already been prepared, a figure of *C. calcarea* has been put in the text. There are two localities entered as "only records," and one of these (Winchcombe) is in Gloucester and not Somerset as given. These can be supplemented by two others; Mr Knight and I saw it on Coldwell Rocks near Symonds Yat in August 1925, and recently a specimen collected by Dr Lloyd Praeger on the Hill of Usinach, West Meath, was sent to me by Miss Knowles. As in so many other lichens the colour of the thallus varies according to the shade and humidity of the habitat, becoming much paler and greener in deep shade. An associated lichen at Coldwell Rocks has been determined by Mr Knight as *Bilimbia albidocarnea* v. *alborubella*, whilst an associate on the Hill of Usinach has been placed under *B. chlorotropoides*. Both these lichens are "only locality" ones in the Monograph, and it is quite probable that they are one and the same plant. If the internal violet coloration, which is sometimes shown in the apothecium of *B. chlorotropoides*, is neglected (its accidental nature is suggested in a note on p. 153) one fails to see what essential character differentiates them. *B. herbidula*, another "only locality" lichen, "a doubtful species perhaps referable to *B. cuprea*" (p. 153) may be discarded or united with *B. chloro-*

tropoides, the size of the spores, as given by Nylander, being much smaller than those of *B. cuprea*. The nature of the supposed algal symbiont is so uncertain that it cannot be taken into account when considering the specific value of the plant, especially as the evidence suggests that the peculiar algal cells noticed by Nylander belonged to an associated or intermixed alga. There is a natural desire to retain species created by well-known lichenologists but this conservatism has been departed from in regard to some of Stirton's species (e.g. *Lecidea amphiplecta* has been included in *L. orphnaeilla*, *L. phyllodisca* in *L. pilati*, and *L. endocyanea* in *L. griseoatra*) and also in such cases as *Lecidea fuscorubens* and *L. ochracea* which are now (p. 45) rightly merged together under the former name. The same procedure also seems advisable with *Lecidea uliginosa* and *L. fuliginea*. The latter is, I think, better regarded "as being only a lignicolous condition" of the former, but the author retains it as a species because of the "generally smaller spores," though (owing to some slip) the length of the spore in *L. uliginosa* is given on p. 32 as shorter than that of *L. fuliginea* (p. 33). So far as I know no experiments have been made to grow spores of *L. uliginosa* on wood or those of *L. fuliginea* on earth, but there is a fair amount of variability in the size of the spore in both "species" and, if this character is taken as the critical one, lignicolous forms of *L. uliginosa* and terricolous forms of *L. fuliginea* occur. The omission of *Lecidea pissodes* and *Endocarpon rugosum* and the notes suggesting the doubtful specific value of *Lecidea declinascens*, *L. sympathetica*, *L. aenea*, *L. dubia* and *L. humigena* seem fully justified.

Some rearrangement has been made in the grouping of some Lecideas. *L. wallrothii* and *L. demissa* have been transferred from the Biatora section into that of Psora; *L. lithophiliza* and *L. submoestula* from Biatora to Eulecidea; *L. mucosa*, *L. cycliska*, *L. nigroclavata* and *L. antiloga* from Eulecidea to Biatora whilst the much-needed and more sweeping transference of *Aspicilia dicksonii* to Eulecidea has been accomplished. *Biatorina lutea* and *B. dilutia*, on account of their trentepohlioid algal symbiont now rank as Gyalectas and *Opegrapha mirifica* is now considered as a Lecanactis. The trentepohlioid nature of the alga certainly justifies the segregation of the two Biatorinas but their spore characters are scarcely those of Gyalecta, and it seems a better plan to insert them under the genus *Microphiale*.

Specific names have been altered in the following cases: *Lecidea misella* to *L. asserculorum*, *L. pleiospora* to *L. geophana*, *L. atrofuscens* to *L. aihrocarpa*, *Bilimbia sabulosa* to *B. leucophaea*, *B. candida* to *B. turneri*, *Verrucaria limitata* to *V. cyanea*, *V. calciseda* to *V. sphinctrina*, *Thelidium incavatum* to *T. auruntii*, *T. nylanderi* to *T. viride*, *T. explicatum* to *T. subrimulatum*, *Arthopyrenia arenicola* to *A. argilospila*, *A. crombeii* to *A. grisea* and *Mycoporum miserrimum* to *M. quercus*, *Lecidea albocoerulescens* v. *alpina* is now merged in *L. phaenterodes*, *L. subsanguinaria* is reduced to the variety *endorhoda* of *L. sanguinaria* and *Porina chlorotica* v. *persicina* now stands as var. *linearis*. *L. contigua* v. *percontigua* is now raised to specific rank and the same course is apparently followed in regard to *L. sylvicola* v. *infidula* which is absent in this second edition. Two of the localities noted in the first edition are now given under *L. bauschiana* but no indication is given as to where the other ten British Museum specimens have been placed.

Too many species still remain "only locality" ones, but it is satisfactory to note that this stigma has been removed from *Lecidea henrica*, *Bacidia chlorotica*, *B. arceutina* v. *hypnaea*, *Biatorina littorella*, *Verrucaria degenerascens*,

V. fuscocinerascens, *Polyblastia schraderi*, *Gongylia viridis*, *Arthopyrenia spilobola* and *A. arenisada*. Additional records have also been added to a number of species for which only a single locality were given previously but which were not labelled as "only locality" species. The following are examples of such species: *Buellia epigaea*, *B. ryssolea*, *B. saxorum*, *B. impressula*, *B. coniops*, *Arthonia insinuata*, *Opegrapha atricolor*, *O. paraxanthodes*, *Verrucaria peloclita*, *V. mutabilis*, *V. latebrosa*, *V. parva*, *Microglaena nuda*. *Lecidea armeniaca*, *L. leptocline* and *Arthopyrenia halodites* now have British localities given for them. There are still over 250 species or varieties (80 of which are labelled "only locality") with only a single locality appended and no additional localities are given for over two hundred other plants. The fact that there are so many single-locality species suggests that there are too many species created and that the knowledge of the distribution of lichens is still very imperfect, collectors of rare species neglecting to send specimens to the national collection at South Kensington. The repetition of the same locality for different plants shows that the British Museum specimens have been collected by enthusiasts who explored their own districts thoroughly and were rewarded by finding what had been formerly considered rare species.

Some names of localities are given wrongly, but in most cases the mistakes are due to the bad penmanship of the collector. Wivelscombe (p. 256) should be Wiveliscombe, Hawbridge (p. 265) Hawkridge, Homer (p. 271) Horner, Bwlebgwyn (p. 325) Bwlch-gwyn, Nerocke (p. 350) Neroche.

A useful list of microfungi recorded as lichens by British lichenologists is given, Vouaux's "Synopsis" having been followed mainly in regard to nomenclature and classification. In this list *Lophothelium acervatum* Stirt. of the first edition is given as *Discothecium acervatum* and *Endococcus exoriens* Stirt. (*Pyrenococcus exoriens* Wheld. and Wils.) as *Phaeospora exoriens*, whilst mention is made of the Abbe's views in regard to the fungal naming of the parasitic species classified under *Lecidea*, *Biatorina*, *Buellia*, *Leciographa*, *Bacidia*, *Arthonia*, *Thelocarpon*, *Obryzum*, *Verrucaria* and *Arthopyrenia*. The list is a fairly complete one though *Odontotrema* and *Myriangium*, which were considered as lichens by Crombie, are not mentioned, neither is *Melaspilea patersoni*, which on p. 248 is stated to be omitted because it is a species of *Schizoxylon*; probably the author does not consider them as coming under the title of microfungi.

In the Addenda an additional *Arthopyrenia*, collected by Miss Knowles at Ballycastle, Antrim, is given. This *A. gyalectoidea* is a very distinct looking plant, especially in the dry state, the immersed perithecia having a gyalectoid appearance.

The last thirteen pages contain an Appendix to Part I and are chiefly occupied by a list of the species of *Crocynia* given as British in Hue and Lesdain's Monograph of *Crocynia* and of those of *Acarospora* which have been added to the British species by Magnusson during the last two years. The following *Acarosporas* are described for the first time in a British Museum Monograph: *A. scyphulifera*, *A. verruciformis*, *A. opaca*, *A. badiofusca*, *A. normanii*, *A. magnussoni*, *A. subrufula*, *A. fusca*, *A. aequatula*, *A. muddii*, and *A. veronensis*. *A. umbilicata* must also be added to the British species as a specimen collected at Symonds Yat in August, 1925, has recently been determined by Magnusson as the form *congregiens* of this species. A *Lecanora* (*L. actophila*) and a *Stenocybe* (*S. bryophila*) are also added. It is of interest

to note that another locality for the latter has been added since it was published in the *Journal of Botany*.

All the 59 plates which were in the first edition are in this, and four plates illustrating *Dirina repanda*, *Roccella fuciformis*, *Pyrenidium actinellum* and *Sarcopyrenia gibba* are added. The paraphyses in *Arthonia radiata* are rather too distinct and septa are not shown in those of *Graphis elegans*. The inscription on Plate 15 should read *Bombyliospora incana* and that on Plate 61 *Mycoporum quercus*.

The thinner paper on which the text is printed makes the book less cumbersome, and the author and others responsible are to be congratulated on having produced an excellent and well got-up book of reference for those interested in this group of plants. Perhaps at some future time it may be possible to combine the text of the two parts (omitting localities) and to issue the plates in a separate volume so as to provide a Handbook more convenient to travel with than the two volumes of the present Monograph.

W. W.

A Census Catalogue of British Mosses with List of the Botanical Vice-counties and their boundaries and Lists of Sources of Records (2nd Edition) compiled for the British Bryological Society by J. B. DUNCAN. 1926. Price 2s. or 2s. 6d., interleaved, post free. To be obtained from Mr W. R. Sherrin, A.L.S., South London Botanical Institute, 323, Norwood Road, London, S.E. 24.

Anyone who desires to study the distribution of mosses in the British Isles can find plenty of interest in this catalogue. All the known British species are listed and for each species the vice-counties in which it is found are enumerated. Numerous additions have been made since the first edition was issued in 1907, but the hope which was expressed in that edition that it would make possible "in the course of a few years...to compile a very fairly accurate and complete statement of Moss Distribution in Britain" has not been fully realised. Many gaps have been filled but a few vice-counties have been very imperfectly worked.

Mr Duncan has spent a great deal of time and energy in working out the distribution in some of the neglected vice-counties. As a supplement to that work he undertook the collection and compilation of the new vice-county records and the issue of this Catalogue bears testimony to the skill and energy by which his task has been accomplished. Not only has he collected and catalogued the new records but in the case of a doubtful record he has examined or submitted to another bryologist the voucher sent in and verified the naming. In many cases the voucher specimen has been submitted to several expert bryologists before it has been allowed to stand. Mistakes have probably crept in, but the method adopted has greatly reduced their probability and therefore the catalogue may claim to be an accurate account of the mosses found in a particular county, though it may not be a complete account of moss distribution in the British Isles.

W. W.

NEW BOOKS RECEIVED

The Student's Handbook of British Hepatics, by SYMERS M. MACVICAR, with illustrations by H. G. Jameson. $8\frac{1}{2} \times 5\frac{1}{2}$ inches. Pp. xxix + 464 + viii. Second edition, revised and enlarged. Eastbourne, Sumfield; London, Wheldon and Wesley. 1926. Price 24s.

Students of the British Liverworts will warmly welcome the new edition of this standard work. It forms an excellent companion volume to Dixon and Jameson's *Students' Handbook of British Mosses* (noticed in this *Journal*, 23, p. 296), which it closely resembles in style, treatment and illustrations of the species. It gives all the information that the ordinary student requires about each species in a clear and concise manner. There is a good introduction, glossary and index.

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STUDIES IN THE ECOLOGICAL EVOLUTION OF THE ANGIOSPERMS

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CHAPTER II

THE ARCHICHLAMYDEAE

INTRODUCTION

IF we adopt the most general viewpoint possible and deduce nothing more from the fossil Angiosperm record than that from Cretaceous times onwards the preserved remains of flowering plants indicate general widespread warm and moist climatic conditions, it seems perfectly reasonable to suppose—at least as a working hypothesis—that, at the present time, ancient types will be found in regions that are still warm and moist and have remained so, as far as geological evidence shows, for a very long period of time. This does not mean that the whole moist tropical flora is of an ancient type. Differentiation does go on under relatively unchanging conditions, as is sufficiently shown by the evolution of life in the sea. Such differentiation may partly be considered to be due to internal forces and thus partly may be entirely independent of the external environment, but in warm, moist, tropical regions, where conditions of life are very favourable, the effect of the living environment (plant competition for space, etc.) is also very important. The latter, of course, acts partly through modifying the inorganic environment, particularly through alterations in the light factor. The animal world, especially the insect world, has also played a part in connection with floral evolution, and in some directions, particularly in the more superficial flower characters, and in types which play a subordinate rôle in the vegetation, this has, in a few cases, proceeded even further in the moist tropics than among allied types in drier subtropical or extratropical regions.

In connection with their vegetative life, tropical plants have become differentiated in various directions. The tree forms vary in

height and, to some extent, in the characters of their wood, their bark, their branching and their leaves, though on the whole remaining of a fairly uniform, tall, hard-wooded, sparingly branched, large-leaved, often leathery-leaved type. The climbing habit appeared very early as is shown by the abundance of woody lianes in many ancient orders and families as well as by the fossil record. The lianes also show progressive evolutionary development from woody types to herbaceous. The herbaceous habit in general is also ancient, as exhibited by the herbs occurring as forest undergrowth and around the forest margins and spreading along river banks and streams.

Minor evolutionary lines of development have resulted in the production of epiphytes (which in many cases connect with the lianes), parasites and saprophytes and families of insectivorous plants.

Emphasis should be laid on the fact that the great lapse of time has allowed the internal forces which influence evolutionary differentiation to produce the various families of flowering plants which (with a number of notable exceptions) are all well represented in the moist tropics. It is true that the general ancient character of the moist tropical flora is shown by such facts as the following:

(a) The relatively primitive Archichlamydeae are proportionately much better represented in the tropics than the relatively advanced Sympetalae.

(b) Nearly all the great tree families of the Angiosperms are predominantly tropical.

(c) Most of the orders recognised as primitive by different schools of thought among systematists are either tropical or, if they extend into extratropical regions, are hygrophilous or show traces of a tropical ancestry. This applies to the Piperales, Salicales, Jugaldales, Myricales, Fagales, Urticales, Ranales, Pandanales, Helobiaeae and Principes.

But from our present standpoint comparatively little useful information is brought to light by attempts to trace the general phylogeny of the Angiosperms as a whole or to seek for connections between the more clearly defined orders and families. Such general phylogenetic schemes must remain, at the present stage of our knowledge to a greater or less extent speculative.

If, however, we accept the assumption that through the long history of the Angiosperms their natural groups have become differentiated, partly through what Osborn has described as the action, reaction and interaction of internal forces, and partly through the similar action, reaction and interaction of the surrounding

plants and animals (the biota), and suppose that the physical environment, because of its relative uniformity had, to begin with, comparatively little effect, then, in our study of phylogeny, we are led to confine our attention, for the most part, to the various narrower circles of affinity, to the families or the best defined orders.

Within such narrower circles of affinity the evidence that the moist tropical flora is older than the flora of drier regions, on the one hand, and of colder regions, on the other, is quite strong and it will be dealt with in detail in the pages which follow. That the extreme climatic differentiation, which began apparently during the latter half of the Tertiary or perhaps only towards its close, has been responsible for the evolution of plant forms adapted to modern dry or cold regions is a perfectly reasonable supposition, but it is not denied that, in many cases, the process began much earlier. The period of lowering of temperatures at the close of the Cretaceous doubtless saw the beginnings of many derivative temperate types. But the fact that it is only within the narrower circles of affinity that, as a rule, it can be shown that the moist tropical types are phylogenetically older than the drier or colder types is very significant.

THE ORDERS AND FAMILIES OF ARCHICHLAMYDEAE

The evidence supplied by phylogeny is evidence which is somewhat difficult to present. Systematists have, on the whole, succeeded wonderfully well in bringing like near to like and in separating types which are fundamentally different, but they have seldom tried to explain the underlying principles that have guided them. We must accept the arrangements and subdivisions that have been arrived at by the various specialists who have dealt with the different families and assume that, so far as the families themselves and the more natural of the orders are concerned, these arrangements are as natural as is possible at the present stage of our knowledge. Our task is easier since we are only concerned with the narrower circles of affinity, and the relationships between the main orders and their arrangement in a general phylogenetic scheme, from our present standpoint, is of less importance. An effort, however, must be made to cover the whole ground, since, though it is easy to select examples which support our theory, selected evidence must always remain unsatisfactory and unconvincing.

Since it is not considered particularly important what scheme of arrangement of the families is followed, Engler's system is adhered to more or less closely. The new system proposed by Hutchinson

(1926) has also been consulted, but interesting though the ideas there set forth are, it may be doubted whether the great stress laid on the difference between the woody and herbaceous habit is quite justifiable. While the general evolutionary trend has been from the woody to the herbaceous, yet the fact that the herbaceous habit can arise quite easily within very narrow circles of affinity, even within the limits of a genus, must always be kept in mind.

The numbers of genera and species included in each group are given in each case but are, of course, only to be taken as approximately correct.

DICOTYLEDONS (8000 genera, 120,000 species): ARCHICHLAMYDEAE (4500 genera, 68,000 species).

The orders belonging to the Monochlamydeae, which are dealt with first by Engler, may or may not be among the most primitive of Angiosperms. As already explained, I do not propose to deal with such questions in detail, but merely to refer to such facts as have a direct bearing on ecological evolutionary history.

The first half-dozen or so of Engler's orders are small and somewhat isolated and, consequently, do not throw much light on our problem. Yet, even among them, certain facts are significant.

SALICALES (2 gen., 200 sp.). The two genera *Populus* and *Salix* are among the earliest known fossil Angiosperms and, at the present time, both favour stream and river banks. According to Laurent (1907) it is always the types of warm climates which are the oldest.

MYRICALES. The only genus *Myrica* (60 sp.) is as old as the poplars and willows and, like them, at the present time, with few exceptions, favours hygrophilous habitats.

JUGLANDALES (6 gen., 40 sp.). Also go back to the Cretaceous; at present distributed over tropical Asia and North temperate regions. The fossil types are nearest to the tropical forms.

FAGALES. Betulaceae (6 gen., 80 sp.) (birch, hazel, hornbeam, alder) and the Fagaceae (5 gen., 350 sp.) (oak, beech, chestnut).

In these families, which include so many of the present day temperate deciduous trees, there are indications that the older phylogenetic forms are the evergreen types of warmer regions. The northern deciduous oaks, for instance, tend to be evergreen in their juvenile forms. Jeffrey (1917) on grounds of comparative anatomy looks upon the evergreen forms as the older. Berry (1916, p. 81) looks on the fossil genus *Dryophyllum*, which was world-wide in Cretaceous times, as the ancestral stock from which the genera *Castanea*, *Castanopsis*, *Pasania* and *Quercus* were derived. The

leaves of *Dryophyllum* were apparently usually of the rather large, coriaceous, evergreen tropical type.

PIPERALES. The Piperaceae (9 gen., 1100 sp.); Chloranthaceae (4 gen., 35 sp.) and Lacistemaee (1 gen., 15 sp.) are tropical forest families; the Saururaceae (3 gen., 5 sp.) are mostly swamp plants. Their habitats are, therefore, all of a primitive nature, but considerable differentiation in the direction of the herbaceous habit has taken place. Some authorities regard the order as very primitive.

URTICALES. Moraceae (60 gen., 1000 sp.), Cannabinaceae (2 gen., 3 sp.), Urticaceae (43 gen., 600 sp.) and Ulmaceae (15 gen., 130 sp.).

In this order the Moraceae consist mostly of trees and are relatively more tropical and more primitive than the allied Urticaceae, which are mostly shrubs and herbs and are more widely distributed. The small, herbaceous family, the Cannabinaceae are obviously derivative and include the hop, *Humulus lupulus* and the widespread weed *Cannabis sativa*. Within the Moraceae, while the majority are tropical, the Artocarpoideae show advance in their complicated receptacles and curved or inverted ovules, and include the large genus *Ficus*, which, though it has a very ancient fossil record, in its modern forms includes species, which have spread into drier and colder regions, and shows a considerable amount of ecological differentiation, including epiphytic species and low-growing suffruticose forms. In the Ulmaceae the drupaceous-fruited Celtidoideae have sometimes endosperm and are more primitive than the winged-fruited Ulmoideae, which have no endosperm. While both tribes extend into temperate regions, the former is, on the whole, distinctly more tropical or subtropical than the latter.

PROTEALES. The Proteaceae (55 gen., 1000 sp.) are a very interesting but somewhat isolated family of uncertain affinities. They are mostly South African and Australian with a few representatives elsewhere, e.g. New Caledonia and South America. In the southern hemisphere their present day distribution is chiefly warm temperate with extensions northwards along the mountain ranges into tropical regions and they may represent a very early type of temperate flora. There are several other families which indicate that the first responses to temperate conditions took place on the mountain ranges of the world, and it is interesting to note that the African mountain ranges are very old, going back to Permian times. According to Engler's arrangement, the Proteales connect with the Santalales; Hutchinson thinks they are allied with the Thymelaeaceae; Balfour was of the opinion that they had affinities with the Rosales (Leguminosae).

SANTALALES. The Olacaceae (27 gen., 160 sp.) are floristically the most primitive in this order and they are a family of tropical trees and shrubs. Hutchinson looks on the "Olacales" as connecting the "Santalales" with the "Celastrales." The Grubbiaceae (*Grubbia*, 4 sp.) are allied, but more advanced Cape heathlike plants—like the Proteaceae, probably an ancient, warm temperate, derived type. The Santalaceae (26 gen., 250 sp.) are distinctly more advanced floristically. Among them the tropical tribe Anthoboleae are the most primitive, having the ovary superior. The other tribes Osyrideae and Thesiae show advance in having the ovary inferior and are distinctly more subtropical and temperate in distribution. The large herbaceous semi-parasitic genus *Thesium* is widespread.

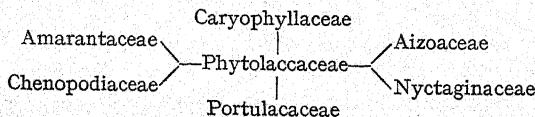
The allied Loranthaceae (26 gen., 900 sp.) show further specialisation in the direction of parasitism but the more tropical tribe Loranthoideae remain, on the whole, more primitive than the Viscoideae. Similarly the Balanophoraceae are highly specialised holoparasites on roots.

The Santalales are a group which illustrate extremely well on the one hand differentiation (chiefly in the direction of parasitism) as a result of the influence of the "biota" or the organic environment, and, on the other hand, response to drier and colder conditions, the influence of the inorganic environment.

ARISTOLOCHIALES. This order also illustrates differentiation resulting from the influence of the biota (*a*) in the Aristolochiaceae (6 gen., 200 sp.) as climbing shrubs and herbs, and (*b*) in the Rafflesiaeae (7 gen., 25 sp.) and the Hydnoraceae (2 gen., 10 sp.) as highly modified parasites.

POLYGONALES. The Polygonaceae (34 gen., 800 sp.) have three subfamilies of which the Rumicoideae with their cyclic flowers are probably to be reckoned the most advanced. The whole family is chiefly north temperate in distribution but the few tropical and southern representatives are, on the whole, relatively primitive phylogenetically, e.g. *Coccloba* which has 125 species in tropical and subtropical America.

CENTROSPERMAE. Pax's arrangement (in Engler and Prantl) of the families in this large order is illustrated by the following diagram:



The central family Phytolaccaceae (24 gen., 120 sp.) are chiefly tropical or subtropical American and African trees, shrubs, or herbs. The Nyctaginaceae (20 gen., 170 sp.), which Hutchinson removes to the Thymelaeales, are also found in the warmer parts of both hemispheres but chiefly in America. They show some advance in the direction of insect pollination, but in the tribe Pisoneae have inconspicuous flowers and straight embryos, an important character in this order where the embryo is usually curved. The Pisoneae are tropical or subtropical trees or shrubs and *Pisonia*, according to the fossil record, goes back to the Cretaceous.

All the other families show interesting and varied degrees of response to the process of climatic differentiation. The Amaranthaceae (56 gen., 500 sp.) have three tribes of which the Celosieae, with two to many ovules, are distinctly the most tropical. The Amarantheae show advance in having the ovules reduced to one, and are more characteristic of dry, subtropical areas. They have produced a number of interesting endemic genera in the semi-desert regions of western South Africa. Others are very common subtropical weeds. The Gomphrenae are most advanced of all in having single ovules together with one-lobed anthers. They are subtropical and temperate in distribution and are still more common as weeds.

The Chenopodiaceae (75 gen., 500 sp.) are closely allied to the Amaranthaceae and are mostly herbaceous halophytes distributed along the seashores of all the continents or in dry regions where the soil is rich in salts or as weeds.

The Aizoaceae (24 gen., 700 sp.) occur in the tropics of Africa, Asia, Australia, and South America, indicating their general tropical origin but they have become most highly differentiated in the drier subtropical regions particularly in South Africa. The Molluginoideae, with the perianth more or less divided and free from the superior ovary, are the most primitive and, at the same time, most mesophytic and tropical. The Ficoideae are a larger subfamily. The tribe Sesuvieae have the ovary superior and occur in the tropics or as seashore plants e.g. *Sesuvium* spp. The tribe Mesembryanthemeae with the ovary inferior are the most advanced especially in the large genus *Mesembryanthemum* with petaloid staminodes which includes over 500 species. [This genus has recently, however, been sub-divided by N. E. Brown.]

Not only floristically is the genus the most advanced in the family but ecologically in its many weird growth-forms it is, in many respects, one of the most highly specialised types of flowering plant. It is particularly characteristic of the dry Karroo region and

desert areas of western South Africa, where the most highly evolved species occur. Species like *M. spinosum* are dominant over wide areas. In no family is the correlation between phylogenetic advance and increasing aridity better demonstrated.

The Portulacaceae (17 gen., 210 sp.) have one or two tropical or subtropical forms, which are relatively primitive, e.g. *Talinella*, two species of Madagascar shrubs with the ovary bilocular instead of unilocular, but the majority are herbs, often annual, and the family, as a whole, is relatively recent and highly evolved. *Portulaca* has the ovary half inferior. The South African *Portulacaria*, a shrub often dominant in dry river valleys, has the ovules reduced to one.

The Caryophyllaceae (79 gen., 1500 sp.) are cosmopolitan but mostly temperate and chiefly herbaceous. The ovary is usually unilocular, owing to the breaking down of the septa between the carpels, but *Telephium*, which has species in Madagascar and the Mediterranean region, has the ovary incompletely trilocular with the ovules basal. The Silenoideae, with gamosepalous flowers are most advanced as regards pollination. They are largely Mediterranean but show wide extensions to other regions and particularly connections with the mountain ranges of the tropics and southern hemisphere. The whole family may be looked upon as a, possibly fairly early, response to temperate conditions in this (Centrospermae) circle of affinity.

RANALES. Whether the members of this order are, as many believe, the most primitive of all Angiosperms or not, there is no doubt that they are at least relatively primitive. The Magnoliaceae (13 gen., 110 sp.) are rich in supposed fossil representatives from the Cretaceous onwards, especially species of *Magnolia* and *Liriodendron*. Though at one time apparently very widespread they are at present confined to warmer regions, especially the south-east of North America and South-East Asia (see Good, 1925). Other large families, also mostly ancient, according to the fossil record, consist of tropical or subtropical or, rarely, warm temperate trees, shrubs, or woody lianes, viz. Menispermaceae (63 gen., 360 sp.), Anonaceae (76 gen., 900 sp.), Myristicaceae (16 gen., 250 sp.), Monimiaceae (30 gen., 250 sp.), Hernandiaceae (4 gen., 25 sp.) and most of the Lauraceae (48 gen., 1180 sp.). This great assemblage of about 250 genera and 3000 species of tropical and subtropical primitive woody plants is sufficiently impressive and by itself lends strong support to our view that the tropical flora is relatively ancient. Within this group of families there are also illustrations of the effects of the biota under tropical conditions in the production of numerous lianes, e.g. most of the

Menispermaceae, while evolutionary advance with increasing aridity or lower temperatures is also shown, e.g. in the Lauraceae, the Perseoideae (anthers 4-locular) are more primitive than the Lauroideae (anthers 2-locular) which include *Laurus* and the parasitic genus *Cassytha*. Similarly the South African genera of the Menispermaceae, *Cissampelos* and *Antizoma* are more advanced floristically than the tropical genera.

Among the more shrubby or herbaceous Ranales, which Hutchinson separates from the Magnoliales at the base of his scheme of phylogenetic classification, there are families, which are generally regarded as derivative and are certainly more temperate in distribution. The Berberidaceae (9 gen., 150 sp.) are chiefly north temperate and show advance in having a definite often trimerous arrangement of parts with the carpels generally reduced to one. They are shrubs or herbs. The Ranunculaceae (32 gen., 1200 sp.) are also usually herbaceous and temperate in distribution though the rather primitive genus *Clematis* is shrubby or climbing and more tropical or subtropical on the whole. Many of the Ranunculaceae are hygrophilous or aquatic. The two families Nymphaeaceae (8 gen., 60 sp.) and Ceratophyllaceae (1 gen., 3 sp.) are entirely aquatic and therefore to be considered derivative. The fact that the former goes back to the Cretaceous shows that the response of the Angiosperms to a purely aquatic environment began very early.

RHOEADALES. This order is, on the whole, more temperate in distribution and shows advance as compared with the Ranales in the cyclic arrangement of the parts of the flower, in syncarpy, etc. The Capparidaceae (43 gen., 450 sp.) are relatively primitive and consist mainly of tropical trees, shrubs or herbs and sometimes climbers. The majority, however, are adapted to rather dry conditions in the tropics and subtropics. The tribe Cleomoideae show transitions to the Cruciferae, a more specialised family (232 gen., 1900 sp.) which are mostly Mediterranean or north temperate in distribution. The Resedaceae (6 gen., 70 sp.) are a small derivative family of mainly Mediterranean xerophytic herbs and undershrubs. The Papaveraceae (30 gen., 600 sp.) are not so closely allied to the Capparidaceae and floristically in some respects are relatively primitive, though they are more specialised in others. They are mostly north temperate in distribution.

SARRACENIALES. In this order Engler includes the Sarraceniaceae (3 gen., 9 sp.), Nepenthaceae (1 gen., 60 sp.) and the Droseraceae (4 gen., 85 sp.) which all illustrate the interesting and well-known

highly specialised response to the effect of the biota in their insectivorous habit, a sideline evolutionary experiment.

ROSALES. Most authorities connect the Rosales more or less closely with the Ranales. The Rosaceae (102 gen., 1700 sp.) are admittedly a somewhat heterogeneous family. The tropical subfamily, the Chrysobalanoideae, though they have retained the woody character, have responded to the influence of their tropical living environment in the zygomorphy of their flowers. The rest of the Rosaceae are mainly temperate or mountain forms. The transition from the woody to the herbaceous type has in some cases e.g. *Alchemilla* been accompanied by marked reduction in their flowers.

Leguminosae (550 gen., 12,000 sp.). The evolutionary history of this great family (cf. Andrews, 1914) in all its numerous details illustrates extraordinarily well the differentiation of primitive tropical forms to suit nearly every kind of modern environment. The relatively primitive Mimosoideae and Caesalpinioideae are mainly tropical but show varied responses to increasing aridity. The more advanced Papilionatae are more temperate, though within this subfamily it is interesting to note that the relatively primitive tribe Sophoreae with the stamens free are still mainly tropical forms from which the more mountain and temperate Podalyrieae may have been derived. There are also a few tropical trees among the Papilionatae, e.g. *Millettia* and numbers of woody lianes, e.g. *Dalbergia*. The Connaraceae (20 gen., 250 sp.) are closely allied and are mostly climbers illustrating again differentiation in response to the biota.

Among the other families of the Rosales the same kind of differentiation is well illustrated. Thus the Pittosporaceae (9 gen., 110 sp.) and the Cunoniaceae (21 gen., 130 sp.) are mostly southern tropical-subtropical families of trees and shrubs, often climbing. The Hamamelidaceae (20 gen., 50 sp.) have an ancient fossil record going back to the Cretaceous and were at one time widespread but are now more restricted in distribution in subtropical and warm temperate regions (Asia, North America and South Africa). The small derivative family Myrothamnaceae (2 sp.) are xerophytic South African shrubs. Similarly the Brunelliaceae (10 sp.) in South America, the monotypic Eucommiaceae in China, the Bruniaceae (12 gen., 55 sp.) heath-like plants in the south-western region of South Africa, are all interesting endemic and probably derivative forms. In another direction the aquatic families Podostemonaceae (27 gen., 120 sp.), Tristichaceae (3 gen., 6 sp.) and Hydrostachyaceae (1 gen., 15 sp.) are highly modified derivative types, illustrating very well, as Willis has shown,

the amount of differentiation that is possible under a relatively uniform environment.

The Saxifragaceae (78 gen., 700 sp.) are allied to the woody tropical Cunoniaceae, but show advance in being shrubby or herbaceous and in the prevalent sinking of the ovary. They are most developed in temperate regions. The Crassulaceae (16 gen., 550 sp.) are in turn allied to the Saxifragaceae. They show response to increasing aridity particularly in South Africa. Within the limits of the large genus *Crassula*, according to Schönland's researches, the relatively mesophytic sections, e.g. *Tillaea* are more primitive floristically than the more xerophytic sections, e.g. *Globulea*.

GERANIALES. In this order a number of tropical woody families, Malpighiaceae (65 gen., 650 sp.), Trigoniaceae (3 gen., 30 sp.), Vochysiaceae (5 gen., 100 sp.), Dichapetalaceae (3 gen., 100 sp.) are tropical woody plants, often climbing. The Erythroxylaceae are a small family of tropical trees (2 gen., 200 sp.) which are allied to the more advanced, more herbaceous and more temperate family Linaceae (9 gen., 150 sp.). Similarly within the limits of the Oxalidaceae (7 gen., 300 sp.) tropical tree forms, e.g. *Averrhoa*, with the fruit a berry, lead on to shrubs, undershrubs and herbs, e.g. *Biophytum* (25 sp.) and the widely dispersed large genus *Oxalis* which has small temperate herbaceous species like the wood sorrel, *Oxalis acetosella*. None of the smaller families illustrate better the normal course of differentiation which, however, is similar to that within the larger families or within several allied families, where the details are sometimes more confusing. The Geraniaceae (11 gen., 500 sp.) are mostly temperate or mountainous in distribution and relatively advanced floristically. Some genera show marked response to increasing aridity in the drier subtropical regions as well, e.g. many species of the large genus *Pelargonium* in South Africa as well as *Sarcocaulon*. The Zygophyllaceae (28 gen., 160 sp.) are another relatively advanced family, including a large number of very xerophytic desert or semi-desert forms.

RUTALES. The Meliaceae (49 gen., 750 sp.), Simarubaceae (30 gen., 150 sp.) and the Burseraceae (13 gen., 400 sp.) are all relatively primitive, tropical, woody families. In the Burseraceae the genus *Commiphora*, which extends into the drier subtropics has the receptacle concave instead of convex, relatively an advanced type. The Rutaceae (125 gen., 950 sp.) include some relatively primitive tropical tree forms but also large numbers of more advanced, warm temperate shrubs, e.g. in the south-western regions of South Africa

and in the Mediterranean region, both important regions in connection with the early beginnings of the temperate flora. The Australian temperate genus *Correa* is interesting, because it has developed sympetaly, giving an indication of a possible starting-point (among forms like the Rutaceae) for the Ericaceae. Hutchinson, however, derives the Ericales from the Theales. The Polygalaceae (11 gen., 700 sp.) are an anomalous family of uncertain affinities included by Engler in the Geraniales, by Rendle (1925) in the Sapindales, by Hutchinson near the "Violales," close to the end of the series beginning with the Rhoeadales. The tropical forms are again the older. The tree genus *Xanthophyllum* is rather isolated but in the tribe Polygaleae the tropical genera *Carpolobia* and *Atroxima* have the petals unappendaged and well developed with the ovary 2- or 3-locular, while the large widespread genus *Polygala* with nearly 500 species is of a more advanced floristic type. The species of the tropical genus *Securidaca* are mostly lianes. The tropical genus *Epirrhizanthes* is holosaprophytic.

TRICOCCAE. The chief family of this order which Engler also includes in the Geraniales is the Euphorbiaceae (270 gen., 4500 sp.). The Buxaceae (7 gen., 60 sp.) are separated by Engler on the characters of the ovules and fruit and the Callitrichaceae (*Callitricha*, 26 sp.) are a small derivative, mainly aquatic, family.

The Euphorbiaceae, like the Leguminosae and other large families, illustrate once more extremely well the process of evolutionary differentiation from primitive tropical forms, towards more advanced types adapted to drier or colder conditions. In the section *Platylobieae*, the *Phyllanthoideae* (ovules 2 per loculus) are a more primitive group than the *Crotonoideae* (ovules 1 per loculus). In the former, the entirely tropical *Daphniphylleae*, with a very short embryo, are the most primitive of all. The slightly more advanced *Brideliae* are still mostly tropical while the still more advanced *Phyllantheae* are more highly differentiated. Within the limits of the single genus *Phyllanthus*, with over 400 species, are included trees, shrubs, undershrubs and herbs, many subtropical or adapted to grassland conditions and drier habitats. The *Crotonoideae* have eight tribes. In the tribe *Crotoneae* the genus *Croton* alone has 600 species of tropical or subtropical often rather xerophytic trees and shrubs in Africa, Asia and South America. The *Jatropheae* and *Adraneae* are tropical. The *Cluyteae* are more subtropical including shrubs and undershrubs adapted to grassland conditions. The *Acalypheae* are still more highly differentiated, including trees, climbers (*Dalechampia*, *Plukene-*

tia, etc.), grassland shrubs and herbs, cultivated and ruderal plants (*Ricinus*) and tender herbaceous plants of the forest undergrowth (*Seidelia*, *Leidesia*, *Micrococca*, *Adenocline*) as well as the temperate genus *Mercurialis*. Most advanced of all in the *Platylobieae* are the *Euphorbieae*, with their peculiar cyathium. Within the tribe, the relatively primitive tropical West African genera *Anthostema* and *Dichostemma* have male flowers with a perianth. Closely allied to *Euphorbia* the West African genus *Elaeophorbia* has the fruit a drupe instead of a capsule. The genus *Euphorbia* with 750 species is in many ways one of the most highly evolved among the Angiosperms. In the moist tropics relatively mesophytic leafy species occur. In the drier subtropics, succulent and thorny species are typical and with reduction in size become extremely common (often dominant) in the semi-desert and desert regions of Africa. Finally the small herbaceous or annual species are the most highly evolved of all and have spread into the temperate regions of the northern hemisphere.

The other section of the family, the *Stenolobieae*, with narrow cotyledons represent a much earlier separation. They are all Australian except one monotype, *Dysopsis glechomoides*, in the Andes with a variety *hirsuta* in Juan Fernandez. Like so many of the early temperate groups, which apparently may have had a mountain origin, the *Stenolobieae* consist of heath-like forms with ericoid or pinoid leaves.

SAPINDALES and **CELASTRALES**. The Sapindaceae (130 gen., 1100 sp.) are the central and largest family of tropical trees and shrubs. Five genera and over 300 species are woody lianes. The Iacacinaceae (48 gen., 200 sp.) are similar and also tropical. The Anacardiaceae (69 gen., 480 sp.) are more differentiated. The tribe Spondieae are relatively primitive in having 3-5 carpels, all with ovules, and are all tropical. The Rhoideae have only one fertile ovule and include the large genus *Rhus* which has spread into the drier subtropical and temperate regions. The tropical genus *Protorhus* is more primitive than either *Rhus* or *Heeria*, the latter a genus of xerophytic subtropical shrubs. The differentiation of the whole tribe from primitive, moist-tropical forms to desert and temperate forms is again most interesting.

The Celastraceae (51 gen., 500 sp.) are again tropical in origin, showing differentiation towards drier and colder conditions. Grouped round these tropical-subtropical woody families of the Sapindocelastral series are a number of smaller families, the Hippocastanaceae (*Aesculus* and *Bellia*) north temperate and South American,

Aceraceae (*Dipteronia* 2 sp. Central China and *Acer*, 115 sp. north temperate), Stackhousiaceae (2 gen., 15 sp.) Australian and New Zealand, xerophytic herbs, Staphyleaceae (*Staphylea* 11 sp.) north temperate, the Balsaminaceae included here by Engler, with the large genus *Impatiens* (340 sp.) tropical and temperate, especially in the mountains of India and Ceylon, Aquifoliaceae (4 gen., 280 sp.) widespread, the Coriariaceae (*Coriaria* 8 sp.) widespread, Empetraceae (3 gen., 4 sp.) north hemisphere and the Andes, Limnanthaceae (2 gen., 5 sp.) North American, all of which show to a greater or less extent advance with increasing response to climatic differentiation. There are also a few small and mainly tropical families, Hippocrateaceae (3 gen., 200 sp.) mostly climbing, Sabiaceae (3 gen., 70 sp.), Melianthaceae (3 gen., 30 sp.), Cyrillaceae (3 gen., 6 sp.), and Pentaphyllaceae (1 gen., 2 sp.). The Salvadoraceae (3 gen., 9 sp.) have sympetaly in *Salvadora*. They are African and Asiatic trees and shrubs.

RHAMNALES. Only two families are included in this order, the Rhamnaceae (50 gen., 500 sp.) and the Vitaceae (11 gen., 500 sp.). The Rhamnales show advance in their marked tendency to unisexuality by abortion and to perigyny or epigyny. The Rhamnaceae in the tropics and subtropics are generally adapted to drier conditions or more open situations and they extend into the temperate regions as well. The Vitaceae are either climbers or shrubs, many of the latter being very xerophytic and cactus-like.

MALVALES. In this order the Elaeocarpaceae (8 gen., 130 sp.) are tropical or subtropical trees or shrubs closely allied with the Tiliaceae (45 gen., 350 sp.) which are both tropical and temperate. The Bombacaceae (22 gen., 140 sp.) are entirely tropical, chiefly American, but include the African baobab (*Adansonia*), a prominent tree of drier regions. The Sterculiaceae (58 gen., 800 sp.) have many ancient tropical tree types but sharply contrasted with them are herbaceous genera showing floristic advance, e.g. *Hermannia* (200 sp.) adapted to open grassland conditions. The Malvaceae (50 gen. 1000 sp.) show floristic advance particularly in the Androecium. A few are moist tropical but the majority are drier subtropical or temperate shrubs or herbs.

PARIETALES. Here the Flacourtiaceae (84 gen., 640 sp.) the Turneraceae (7 gen., 100 sp.), Winteraceae (4 gen., 8 sp.), Cochlospermaceae (3 gen., 20 sp.) and *Bixa orellana*, the only species of the Bixaceae, are predominantly tropical and subtropical woody plants. In the Flacourtiaceae many genera extend into the drier subtropics

but Warburg (in Engler and Prantl) derives all the tribes from the Erythrospermeae which are tropical, another independent testimony in favour of our general theory.

Contrasted with the tropical group once more, a number of more advanced smaller, allied families have a temperate or mountain distribution, the Cistaceae (7 gen., 140 sp.) north temperate shrubs and herbs, the Malesherbiaceae (1 gen., 25 sp.) herbs and undershrubs of western South America, the Loasaceae (13 gen., 230 sp.) mostly herbs, sometimes twining, of the Andes region.

The suborder Tamaricinae show advance in having exendospermic seeds or a little endosperm which is starchy. They include the Elatinaceae (2 gen., 35 sp.) herbs or water plants, Frankeniacae (4 gen., 64 sp.) halophytes, and Tamaricaceae (4 gen., 90 sp.) also mostly halophytes, all specialised and derivative types.

The Passifloraceae (13 gen., 380 sp.) and the Achariaceae (3 gen., 3 sp.) show response to the biota in their climbing habit. They have rather advanced floral structure.

In the Peponiferae, the Cucurbitaceae (100 gen., 800 sp.) may come here. Engler places them among the Sympetalae. In any case, they are another advanced family, under the influence of the biota. Similarly the Begoniaceae (5 gen., 450 sp.) show the effects of competition for space. They are herbs of the forest undergrowth. The exact affinities of the family, however, are obscure. This applies also to the Violaceae (18 gen., 450 sp.) which are included here by Engler. Within the limits of this family, the tropical and subtropical woody Rinoreae, with regular flowers are more primitive and contrast strongly with the temperate herbaceous Violeae, which have irregular flowers.

The GUTTIFERALES, included by Engler in the Parietales, are largely tropical, and contain the Dilleniaceae (14 gen., 320 sp.), the Ochnaceae (22 gen., 250 sp.), the Guttiferae (50 gen., 850 sp.), the Dipterocarpaceae (19 gen., 340 sp.), the Theaceae (20 gen., 200 sp.), the Marcgraviaceae (5 gen., 50 sp.). Advance and differentiation, however, are again shown in the production of lianes and epiphytes (Marcgraviaceae), in shrubs adapted to drier conditions (Ochnaceae), in herbs which become widespread and temperate, e.g. *Hypericum* (Guttiferae).

OPUNTIALES. Cactaceae (23 gen., 1500 sp.). The affinities of this family of highly specialised succulents are quite uncertain. They are all American except *Rhipsalis cassytha*, which is often epiphytic or grows on rocks and is widely dispersed in the tropics of the old world.

MYRTIFLORAE. In this order union of the styles, sinking of the ovary, exendospermy and other features all show advance. None of the families are very primitive though Guppy looks on the prevalent vivipary of the Mangroves (some of the Rhizophoraceae) as a primitive character. The Rhizophoraceae (18 gen., 60 sp.), the Lecythidaceae (19 gen., 250 sp.) are families of tropical trees mostly hydrophilous. In the Combretaceae (17 gen., 450 sp.) the West African tropical Strephonematoideae are primitive in having the ovary only half inferior. The more advanced Combretoideae are characteristic of the drier regions. They also include climbers (e.g. *Quisqualis*). The Myrtaceae (76 gen., 3000 sp.), as in the case of the Leguminosae, Euphorbiaceae and several other large families, illustrate our general theory extremely well (cf. Andrews, 1913). The Myrtoideae are, on the whole, more tropical or more hydrophilous than the Leptospermoideae, which are distributed more over drier subtropical areas, especially the large genus *Eucalyptus* in Australia. Both subfamilies, however, show some degree of response to climatic differentiation. In the Leptospermoideae, the large genus *Eugenia* with over 600 sp. is widespread over the tropics and subtropics of both worlds and shows a range of forms from large trees down to slightly woody undershrubs. *Myrtus communis* is the only European representative.

In the large but very natural tropical and subtropical family, the Melastomaceae (170 gen., 2800 sp.), the range of forms includes trees, shrubs, climbers, epiphytes, herbs, marsh and aquatic plants, another interesting field for the study of differentiation.

As in the other cases, the more purely herbaceous families of the Myrtiflorae contrast with the woody families in being more temperate in distribution and more advanced floristically, e.g. the Onagraceae (39 gen., 500 sp.), chiefly north temperate, Halorrhagaceae (7 gen., 150 sp.) widespread marsh or aquatic plants and Hippuridaceae (*Hippuris vulgaris*) aquatic. The Lythraceae include some tree forms, tropical or subtropical, and derivative herbs often with reduced flowers, cosmopolitan or temperate.

The THYMELAEINEAE are included by Engler as a suborder of the Myrtiflorae. The Thymelaeaceae (41 gen., 450 sp.) are the central family, allied perhaps to the South African woody genus (*Olinia*, 7 sp.) of the Oliniaceae. Among the Thymelaeaceae the tropical West African genus of trees *Octolepis* is the most primitive, having a flat receptacle and the ovary 4-5-locular. The Aquilarioideae and Phaleroideae have the ovary bilocular and are spread over the Indo-Malayan region, China, Australia, the Philippines and tropical

Africa. The most advanced subfamily is the Thymelaeoideae with the ovary unilocular and a much hollowed receptacle. They consist of shrubs, undershrubs, often heath-like, and herbs, distributed over the drier subtropical regions, especially South Africa, and in the genus *Daphne* reaching Europe.

Allied to the Thymelaeaceae and also often heathlike are the small south-western Cape families, Penaeaceae (5 gen., 35 sp.) and *Geissoloma* (Geissolomataceae) as well as the north temperate Eleagnaceae (3 gen., 35 sp.).

UMBELLIFLORA. The Araliaceae (55 gen., 660 sp.) are chiefly tropical and subtropical trees and shrubs and they contrast with the more advanced and mostly herbaceous and temperate family, the Umbelliferae (270 gen., 2700 sp.). Such a pairing between large well-defined families illustrates extremely well the relationship between the tropical and temperate floras. The Cornaceae (10 gen., 100 sp.) are not so closely related to the Araliaceae but they do show floristic advance and are distributed over the temperate regions and mountains of the tropics. They possibly represent a rather ancient temperate type.

SUMMARY

1. Ecological differentiation among the Angiosperms is regarded as having taken place, first of all and for the longest period of time, under relatively unchanging moist tropical conditions. Such differentiation may be due to internal forces, and in so far as this is the case may be entirely independent of the external environment. Under favourable conditions, however, the living environment or biota is important.

2. The great lapse of time since the Angiosperms appeared, during which warm, moist, favourable conditions have prevailed in the tropical regions, has allowed of the differentiation of the great family groups and, under the influence of the biota, of the following main types of plant form, trees (evergreen, hard-wooded, sparingly branched, leathery-leaved, large-leaved), lianes (progressing from the woody to the herbaceous), epiphytes, mesophytic shrubs, undershrubs and herbs of the forest undergrowth and forest margins, as well as still more specialised forms, parasites, saprophytes, and insectivorous plants.

3. More recent climatic differentiation has been responsible for the production of types of plant form adapted to drier conditions, on the one hand, and colder conditions on the other. Some rather ancient temperate types appeared very early, apparently chiefly on

mountain ranges, and in the southern hemisphere. The Mediterranean region is also an important centre for certain temperate groups. Since differentiation in response to increasing aridity and lower temperatures has been on the whole relatively recent, it follows that evidence in support of the view must be sought for in the narrower circles of affinity, the more well-defined orders, the families and some of the larger genera.

4. Since any selected evidence must remain unconvincing, it is necessary to pass in review all the families of the Angiosperms; considerations of space have made it necessary to do so in a somewhat condensed form. Previous writers have done so in greater detail for some of the larger families and particularly Andrews for the Leguminosae and Myrtaceae. The main facts referred to in this paper are set forth in the form of a table in the following appendix.

APPENDIX

Systematic position	Relatively primitive, tropical to subtropical, hygrophilous or mesophytic	Relatively advanced, more temperate or more xerophytic
1. Fagales	Evergreen forms	Deciduous forms
2. Urticales	Moraceae	Cannabinaceae
3. Urticales	Moraceae	Urticaceae
4. Ulmaceae	Celtidoideae	Ulmoidae
5. Santalales	Olacaceae	Grubbiaceae
6. Santalales	Olacaceae	Santalaceae
7. Santalaceae	Anthoboleae	Osyrideae
8. Santalaceae	Anthoboleae, Osyrideae	Thesieae
9. Loranthaceae	Loranthoideae	Viscoideae
10. Polygonaceae	Coccoloboideae	Rumicoideae
11. Centrospermae	{ Phytolaccaceae Nyctaginaceae	Amarantaceae
		Chenopodiaceae
12. Amaranthaceae	Celosiaeae	Aizoaceae
13. Aizoaceae	Molluginoideae	Portulacaceae
14. Ficoideae	Sesuviae, Aizoeae	Caryophyllaceae
15. Aizoaceae	Other genera	{ Amaranteae Gomphrenoideae
16. Portulacaceae	Other genera	Ficoideae
17. Ranales	{ Magnoliaceae Anonaceae, Menispermaceae Myristicaceae, Monimiaceae	Mesembrianthemaee
		Mesembrianthemum
		Portulaca, Portulacaria
18. Menispermaceae	Lauraceae	{ Berberidaceae Ranunculaceae
19. Lauraceae	Other genera	Nymphaeaceae
20. Ranunculaceae	Perseoideae	Ceratophyllaceae
21. Archichlamydeae	Clematis	Cissampelos, Antizoma
22. Rhoeadales	Ranales	Lauroideae
23. Capparidaceae	Capparidaceae	Other genera
	Capparidoideae	Rhoeadales
		{ Cruciferae Resedaceae
		Cleomoideae

	Systematic position	Relatively primitive, tropical to subtropical, hygrophilous or mesophytic	Relatively advanced, more temperate or more xerophytic
24.	Rosaceae	Woody genera (Mimosae (Caesalpinoideae) Sophoreae	Herbaceous genera
25.	Leguminosae	(Pittosporaceae Cunoniaceae Hamamelidaceae Tillaea sect.	Papilionatae
26.	Papilionatae		Other tribes
27.	Rosales		(Myrothamnaceae Brunelliaceae, Bruniaceae Saxifragaceae, Crassulaceae <i>Globulea</i> sect.
28.	<i>Crassula</i>		(Linaceae Oxalidaceae Geraniaceae Zygophyllaceae
29.	Geriales	(Malpighiaceae Erythroxylaceae	<i>Erythroxylon</i> <i>Oxalis</i>
30.	Erythroxylaceae	<i>Aneulophus</i>	
31.	Oxalidaceae	<i>Averrhoa</i>	
32.	Rutales	(Meliaceae Burseraceae Simarubaceae)	Rutaceae
33.	Burseraceae	Tropical genera	<i>Commiphora</i>
34.	Rutaceae	Tropical trees	(Mountain and temperate shrubs
35.	Polygalaceae	<i>Carpolobia, Atroxima</i>	<i>Polygala</i>
36.	Euphorbiaceae	Platylobieae	Stenolobieae
37.	Platylobieae	Phyllanthoideae	Crotonoideae
38.	Phyllanthoideae	Daphniphyllae	Other tribes
39.	Phyllanthoideae	Bridelieae	Phyllantheae
40.	Crotonoideae	(Crotoneae, Jatropheae) (Adrenaeae	Clusiaceae
41.	Crotonoideae	(Crotoneae, Jatropheae) (Adrenaeae	Acalypheae
42.	Euphorbiaceae	All other tribes	Euphorbieae
43.	Euphorbieae	(<i>Anthostema</i> (<i>Dichostemma</i>)	<i>Euphorbia</i>
44.	<i>Euphorbia</i>	Tropical species	(Desert and temperate species
45.	<i>Euphorbia</i>	Perennials	Annuals
46.	(Sapindales Celastrales	(Icacinaceae (Sapindaceae	(Anacardiaceae Celastraceae
47.	Anacardiaceae	Spondiaceae	Rhoideae
48.	(Sapindales Celastrales	(Icacinaceae, Sapindaceae (Celastraceae	(Aceraceae Hippocrastanaceae Aquiloliaceae
49.	(Sapindales Celastrales	(Icacinaceae, Sapindaceae (Celastraceae	(Stackhousiaceae (Staphylaceae
50.	(Sapindales Celastrales	(Icacinaceae, Sapindaceae (Celastraceae	(Coriariaceae Empetraceae Limnanthaceae
51.	Archichlamydeae	(Sapindales, Celastrales) Geranioides	Rhamnales
52.	Malvales	Elaeocarpaceae	Tiliaceae
53.	Malvales	Sterculiaceae	Malvaceae
54.	Sterculiaceae	Tropical trees	<i>Hermannia</i>
		Flacourtiaceae	(Cistaceae Malesherbiaceae
55.	Parietales	Turneraceae Winteranaceae Bixaceae	(Loasaceae
56.	Parietales	Flacourtiaceae Turneraceae Winteranaceae Bixaceae	(Elatinaceae Frankeniacaceae Tamaricaceae

Systematic position	Relatively primitive, tropical to subtropical, hygrophilous or mesophytic	Relatively advanced, more temperate or more xerophytic
57. Flacourtiaceae	Erythrospermeae	Other tribes
58. Violaceae	Rinoreae	Violeae
59. Guttiferales	Tropical genera	<i>Ochna, Hypericum</i>
60. Myrtiflorae	{ Rhizophoraceae } Lecythidaceae }	Combretaceae
61. Combretaceae	Strephonematoideae	Combretoidae
62. Myrtaceae	Myrtoideae	Leptospermoideae
63. <i>Eugenia</i>	Tree forms	Undershrubs
64. Myrtiflorae	{ Myrtaceae Melastomaceae }	{ Onagraceae Halorrhagaceae }
65. Lythraceae	Tree forms	Herbaceous forms
66. Thymelaeaceae	<i>Octolepis</i>	All other genera
67. Thymelaeaceae	{ Aquilarioideae } Phalerioideae	Thymelaeoideae
68. Thymelaeinae	Thymelaeaceae	{ Penaeaceae Geissolomataceae }
69. Umbelliflorae	Araliaceae	Eleagnaceae
70. Umbelliflorae	Araliaceae	Umbelliferae
		Cornaceae

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(To be continued)

MYCORRHIZA

By M. C. RAYNER

CHAPTER X

Tuberisation: The association of root nodules or tubercles with fungus infection—Historical—Nodules of leguminous plants: early views—Root nodules of *Alnus*, *Eleagnus*, *Myrica*, *Ceanothus*: early observers; Bottomley; Spratt—The root tubercles of Cycads—Root nodules of *Podocarpus* and other Conifers: Spratt; McLuckie; Yeates. The tuberisation theory: Bernard; Magrou.

OBSERVATIONS associating the presence of fungus mycelium with the formation of nodules or tubercles are not uncommon in the literature of root infection and merit brief notice, albeit many of the earlier records betray inaccuracies due to faulty observation and still more faulty technique.

Malpighi (1679) figured small nodules on the roots of legumes, mistaking them for insect galls, and similar observations were made by Duhamel (1758). Meyen (1829) noted the root tubercles of Alder and believed them to be parasites similar in habit to members of the Orobanchaceae, although of more lowly development. Schacht (1853, 1860) also observed these conspicuous outgrowths on Alder roots, regarding them first as normal and afterwards as abnormal outgrowths, but he made no attempt to explain their presence. Woronin (1866) believed that the organism present belonged to the genus *Schinzia*, founded by Nägeli for a mycelium observed in Iris roots; he named it, accordingly, *S. alni*. Later, following a paper by Gravis (1879) on the same subject, he reinvestigated the structure of young nodules, and found in the cells an organism believed to be identical with his previously described *Plasmodiophora brassicae* in Turnip. Woronin concluded that both a Myxomycete and a filamentous fungus were constantly present in the nodules of Alder, a belief which Gravis (1885) endorsed in a subsequent paper.

Warming (1876) noted similar "galls" in *Hippophae*, *Eleagnus* and *Shepherdia*, and discovered in all cases an organism resembling the "*Plasmodiophora*" of Woronin. Möller (1885), after repeating once again the observations on Alder, named the endophyte *P. alni*, but Woronin adhered to his original view that a filamentous fungus was also present.

The confusion caused by all these conflicting views was partially cleared up by Brunchorst (1886), who, by the use of improved methods,

showed that the so-called "plasmobia" were actually the cell protoplasts, imbedded in which were fine filaments believed to be fungus hyphae. The bodies mistaken for spores by Woronin and Möller he held to be sporangia.

Brunchorst referred the fungus in Alder nodules to a genus distinct from *Schinzia*, proposing for it the new generic name, *Frankia*. Unfortunately he rejected the well-known specific designation and renamed the organism *Frankia subtilis*; he regarded the mycelia present in the nodules of the various other plants mentioned as belonging to the same fungus. Subsequently, Woronin accepted Brunchorst's views on Alder nodules in the main, though still differing in respect to the interpretation of certain details of structure, and incidentally, caused further confusion by giving the name *Frankia brunchorsti* to the organism present in *Myrica gale*.

Equal disagreement existed in respect to the significance of these structures. In Alder, Ward (1887) believed that the mycelium was responsible for certain changes appearing in the cytoplasm of the host cells. Frank (1887) rejected the view that the nodules were due to parasitic invasion, and expressed the opinion that they were normal organs functioning for the transitory storage of proteins. In view of the existing confusion he further suggested that the names *Schinzia alni*, *Plasmodiophora alni*, *Frankia subtilis* and *Schinzia leguminosarum* should be deleted from mycological literature!

Weber (1884) examined the root nodules formed by the Toad Rush (*Juncus bufonius*), and referred to certain earlier observations by Magnus, who had described a mycelium present in the roots of this species and also in those of *Cyperus flavescens* under the name of *Schinzia cypericola*.

The structures produced by the Toad Rush resemble miniature Potato tubers (Fig. 53). Formed only by certain individuals, it is at present an open question if they should be regarded as a varietal character or as a response to soil or other external conditions. Their precise morphological nature is not clear from the published accounts, while the possible existence of a causal relation with fungus infection requires experimental investigation.

Frank (1891) expressed the opinion that the root nodules of Alder and of members of the Leguminosae were biologically related to mycorrhiza. Since they appeared to be structures morphologically distinct from roots, he proposed that they should be named "Mykodomatien." The exact nature of the endophyte was in some doubt. While expressing the view that the filaments resembled those of a

bacterium belonging to the *Leptothrix* group, he evidently inclined to the view that they were fine hyphae. In the case of certain legumes, e.g. *Phaseolus vulgaris*, he held that the nodule organism was purely parasitic. In the same paper Frank (1891) elaborated his conclusions in respect to "Pilzsymbiosis" in general, enumerated the families in which mycorrhiza had been observed, and noted that the true nature of the "Rhizobia" was, in most cases, still unknown. Much controversy took place at this time and later respecting the real nature of the "Infectionsfäden" in the tissues of leguminous nodules.

Schneider (1892) made observations upon American "Rhizobia" and published a scheme of classification to include the forms observed in different species. He contributed his own views to the controversy respecting the exact nature of the nodule organisms, which, by that time, had been described by Woronin as "Bakterien," by Brunchorst as "Bakteroiden," by Ward (1889) as "spores" or "gemmales" and by Beijerinck (1890) as a specific bacterium, *Bacillus radicicola*. Subsequently he published an historical survey of the history of leguminous nodules and the literature concerning fixation of atmospheric nitrogen by plants, while Bottomley (1907), contributed to that dealing with the morphology of root nodules in general.

When Hellriegel and Wilfarth brought to a close a long series of experiments dating back to 1862 and put forward their new hypothesis respecting the nitrogen-assimilating powers of leguminous species, they established experimentally two essential facts. One, the direct relations between nodule formation and the ability of legumes to utilise atmospheric nitrogen: the other, the dependence of the nitrogen-fixing capacity on the activities of organisms present in the nodules.

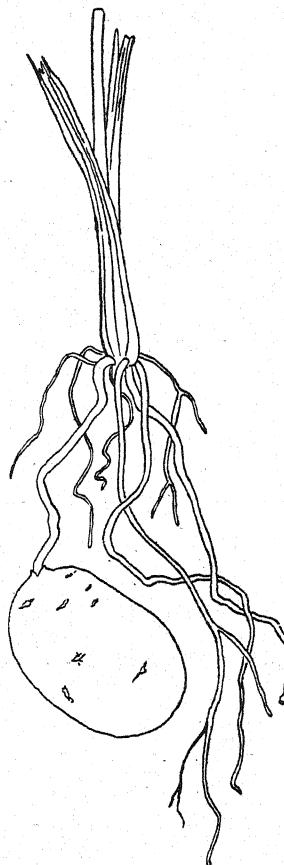


Fig. 63. *Juncus bufonius*; basal part of a plant showing root system and a single tuber.

It is outside the scope of the present review to attempt a survey of the voluminous literature dealing with the root nodules of leguminous plants. Some mention of the subject is called for in an historical account of work on root infection, because the earlier observers commonly attributed the formation of root nodules—whether by members of Leguminosae or of other groups—to endotrophic fungus infection similar to that in mycorrhizas. Of recent publications dealing with various aspects of the subject may be mentioned papers by Spratt (1919), Lohnis and Hansen (1921), Bewley and Hutchinson (1920), and Wright (1925).

Nodules very similar in appearance to those of legumes are formed not only by Alder, but also by species of *Eleagnus*, *Ceanothus*, and *Myrica*. Hiltner (1896) had reported the presence of bacteria in the root nodules of Alder and *Eleagnus*, and demonstrated experimentally that young Alders without nodules did not thrive in soils poor in nitrogen, whereas inoculation by the appropriate organism was followed by nodule formation accompanied by greatly increased growth. He had noted also that the production of nodules was more active in poor soils, and inferred that the numbers produced by Alder under conditions of nitrogen deficiency could be used as a measure of the activity of the tree in respect to nitrogen fixation. The nodules in the roots of *Ceanothus americanus* were examined by Beal (1890) and Atkinson (1892), the latter of whom named the organism present *Frankia ceanothi*. Later, Bottomley (1915) re-investigated them and, in the light of his own work on similar structures in other plants, reported that they represented modified lateral roots infected by a bacterium belonging to the *Pseudomonas* (*Bacillus*) *radicicola* group.

The work of Shibata (1902) on *Alnus incana* and *Myrica gale* has already been noted. Although he inferred infection by fungus mycelium in the roots of both species, this author noted that in *Alnus* the structure of the thread-like "hyphae" was bacterial in character, while in *Myrica* he suggested that the endophyte was related to *Actinomyces* rather than to the Fungi proper.

From root nodules of the same species, Peklo (1910) isolated an organism which he identified as a species of *Actinomyces*, but attempts to reproduce nodule formation by means of inoculation were not attended by success. More recently, Dufrénoy (1920) has recorded *Actinomyces* sp. as an endophyte in roots and shoots of *Adenostyles albifrons* in the Pyrenees, and expressed the view that shoot infection of a similar type likewise occurs in members of Compositae, Orchid-

aceae and Ericaceae, although further work is required to establish this claim.

The nodules of *Myrica* were subsequently investigated by Bottomley (1912) who reported infection by a nitrogen-fixing organism belonging to the *Pseudomonas radicicola* group. Old nodules and the basal regions of younger ones were subject likewise to occasional infection by mycelial fungi.

The curious coraloid roots produced by all genera of living Cycads have often attracted attention. They were studied by Reinke (1872), Schneider (1894), Life (1901) and Zach (1910). According to Spratt (1915), the initial stimulus to their formation is due to infection by *Pseudomonas radicicola*. Later, they suffer multiple invasion by other micro-organisms—invariably by species of *Azotobacter*, frequently also by species of *Anabaena* that give rise to the characteristic algal zone.

Mention has been made of the nodular roots formed by *Podocarpus*. Experimental enquiry convinced Nobbe and Hiltner (1899) that these structures were actively concerned in the fixation of atmospheric nitrogen. Thus, they found it impossible to cultivate young plants of *Podocarpus* in quartz sand lacking combined nitrogen in the absence of the organism responsible for nodule formation, whereas plants possessing nodules made healthy growth during five years' cultivation in like conditions.

Shibata (1902), working on two Japanese species of *Podocarpus*, identified what he believed to be the mycelium of a mycorrhizal fungus in the root tissues; he described in detail the cytological changes brought about by the digestion of the intracellular mycelium, and demonstrated the presence of active proteolytic enzymes by means of glycerine extracts of the nodule tissues.

The nodules produced by *Podocarpus* and other members of the Podocarpaceae are characteristic in appearance and arrangement, giving a curious "beaded" appearance to the affected roots. Their morphology and physiological significance was studied by Spratt (1912) who reported the presence of nodules of similar type in *Podocarpus*, *Microcachrys*, *Dacrydium*, *Saxegothaea*, and also in *Phyllocladus*, a genus whose systematic affinities have aroused some controversy. In all the genera examined, they were reported to be perennial structures formed by the modification of lateral roots following infection by nitrogen-fixing organisms identical in structure and behaviour with the strains of *Pseudomonas radicicola* extracted from the root nodules of leguminous plants and also from those of

certain non-leguminous species. The majority of the cortical cells undergo some structural modification and give rise to a characteristic water-storage tissue, in certain cells of which the endophyte may remain dormant during the winter. In a subsequent paper, Spratt (1919) reviewed the whole subject of nodule formation, and summarised the experimental evidence on which were based the conclusions reached by herself and by Bottomley, in respect to the identity of the nodule organism in all the cases just cited.

If the views of these observers are accepted, it may be assumed that the root nodules of *Alnus*, *Myrica* and members of the Eleagnaceae, Ceanothaceae, Cycadaceae, and Podocarpaceae play a rôle in the economy of their vascular hosts similar to that securely established for the corresponding structures provoked by the presence of the nodule bacteria in roots of legumes.

In a series of papers entitled "Studies in Symbiosis" McLuckie (1923 a) has recently contributed his observations on the nodular roots of certain Australian species of *Podocarpus* and *Casuarina*. He has confirmed the opinion expressed by Spratt that those of *Podocarpus spinulosa* and *P. elata* are due to infection by a bacterium showing many points of resemblance with *Pseudomonas radicicola* although not certainly identified with that species. In pure culture outside the plant, the organism present is reported to fix atmospheric nitrogen at the rate of 6 to 7 mg. of nitrogen per 100 c.c. of nutrient solution in 21 days. In *Podocarpus*, the cortical cells of the main roots and those of some of the nodules were observed likewise to contain mycelium of a mycorrhizal type.

The root nodules of *Casuarina cunninghamiana* were reported by McLuckie to be due to infection by a similar type of nitrogen-fixing bacterium to that isolated from *Podocarpus*. In another species, *C. equisetifolia*, from coral islands near Java, the roots bear structures resembling the nodules of Alder. These were examined by Miehe (1918) and found to consist of closely compacted masses of freely branched, shortened rootlets, in certain cortical cells of which fungal hyphae were present. The tubercles were reported on the roots of all individuals growing in a natural habitat but were not observed on those in cultivation in Europe. They were named "*Rhizothamnion*" by Miehe who believed that they represented a typical case of beneficial symbiosis in which the fungus partner functioned by converting nitrogenous materials in the humus into forms directly available to the vascular host. In view of the possibility of mistaking the zoogloea threads of a bacterial endophyte for fungal hyphae, and

the uniformity of all recent records associating a nitrogen-fixing organism of the *Pseudomonas radicicola* type with root nodules, confirmation of Miche's observation on *Casuarina* would be welcomed.

Yeates (1924) has made a further contribution to the subject of root nodules in conifers, based upon observations made on species indigenous to New Zealand. He reports nodule formation by "all the New Zealand pines" with the exception of two species of *Libocedrus*. He found them also on several members of the Araucarineae including the Kauri Pine (*Agathis australis*), on which they had been noticed previously by Cockayne (1921). In respect to the morphology of the nodules and their function as organs for water storage, Yeates' observations and deductions agree with those of Spratt. In this connection, the former has noted that the size of the juvenile leaves in species of *Dacrydium* and *Podocarpus* is roughly proportional to that of the root nodules, i.e. the forms with larger leaves showing also the greatest development of water-storage tissue. Moreover, the species showing the smallest nodules are likewise those in which the transition from the large juvenile type of leaf to the reduced form characteristic of the adult, is most striking, e.g. *Dacrydium biforme*: "In other words, absence of sufficient water-tissue on their roots has compelled these species to reduce their leaf-surface and so to economize their water supply"—an argument cogent enough in itself although expressed in somewhat teleological form. From his examination of the mycorrhiza of *Cunninghamia*, *Libocedrus*, and *Cupressus*, Yeates is prepared to extend this hypothesis to conifers generally, in the form that root reduction consequent upon mycorrhizal infection is accompanied by parallel diminution in size of the leaves.

His thesis that the Abietineae constitute an isolated case in which absence of endophytic mycorrhiza is correlated with a tendency towards persistence of the juvenile leaf habit, is hardly borne out however by the recent observations of Melin (see Chap. VIII) on the mycorrhiza of Spruce and Pine.

In respect to the characters of the nodule organism in Taxads, the observations of Yeates are markedly at variance with those of Spratt. The vast majority of nodules investigated by the former are reported as showing infection by the characteristic type of mycorrhizal fungus with non-septate mycelium and vesicles; only in less than 1 per cent. of some hundreds of nodules examined did he observe bacteria similar to those figured by Spratt and also by McLuckie for *Podocarpus*. Yeates has concluded that the nodules

function primarily as organs for water storage and are also beneficial to the trees by enabling them to draw indirectly upon the organic residues present in the soil through the agency of their mycorrhizal fungi.

Reviewing the cases described, it may be concluded that there is evidence that the formation of nodules by a number of plant species other than legumes is directly related to invasion of the roots by strains of a bacterial organism closely related to *Pseudomonas radicicola*. Whether this conclusion can be extended to include the Podocarpeae and other nodule-forming conifers is at present doubtful, and requires confirmation by means of pure culture experiments on the species concerned. For example, in view of the conflicting nature of the observations made by Spratt and Yeates respectively, it would be desirable to investigate the response shown by *Podocarpus* seedlings to independent infection by the bacteria isolated from the nodules.

On the other hand, evidence is not lacking that tuberisation, in greater or less degree, is often a consequence of fungal infection. The "Knollenmycorrhizen" of Pine and Fir (see Fig. 50) may be cited as a case in point and in external features these bear some resemblance to the nodular roots of Alder and Cycads. It was, indeed, the constant association of local hypertrophy with endophytic infection by mycelium that led Bernard (1902) to put forward the theory of tuberisation subsequently extended and elaborated by Magrou (1921) and others. A short account will now be given of this interesting and far-reaching hypothesis, with a critical examination of the evidence adduced in support of it.

Laurent (1888) had shown that tuberisation in plants could be provoked experimentally by raising the concentration of the culture medium. Bernard's attention was attracted to the subject during his early observations on the Ophrydeae, in members of which group the formation of tubers is so constant and regular that their morphology can be utilised as a basis of classification. He was struck by the prevalence of the habit among herbaceous perennials in general and, finding no clue in Laurent's work to the stimulus provoking tuberisation under natural conditions, he looked around for a cause "as widespread as the habit." He was familiar with the prevalence and constancy of the mycorrhizal habit in wild perennials and also with Stahl's observation that species producing bulbs and tubers are specially prone to infection. His own researches on members of the Ophrydeae convinced him that a causal relation between fungus invasion and tuberisation existed in members of this group.

So, by more than one line of reasoning, he was led to the view that tuberisation (or its equivalent) and, in general, the perennial habit in herbaceous plants, represents a condition of relatively advanced adaptation to communal life between vascular plants and fungi, and is in itself a direct consequence of such a symbiotic relation. With this theory was bound up an equally speculative hypothesis tracing the evolution of vascular plants from thalloid members of Bryophyta as an indirect consequence of fungal infection and the establishment of the perennial habit in the latter.

The evidence collected by Bernard from observations on *Ophrys* and allied Orchids may be briefly summarised as follows. Seed germination leads to the formation of a small tuberous structure, the primary tubercle, bearing an apical bud and showing profuse infection by mycelium at the basal end. During the first season's growth, the bud produces a few leaf rudiments and a lateral swelling—the first tuber—which is eventually set free in the soil. The primary tubercle dwindles and disappears, while the tuber, still entirely free from fungus infection, gives rise, during the ensuing vegetative season, to a short axis bearing absorptive hairs. The latter quickly become infected from the soil, as may later the tuber itself. The same sequence is repeated annually until the seedling reaches maturity. In the autumn preceding flowering, the roots, produced at the end of September, become infected from the soil and remain in this condition until their death after flower production in the following spring. One or more of the axillary buds then develop to a tuber or tubers, and the plant remains free from infection until the new roots are produced in the early autumn. Thence onwards this regular annual periodicity persists as a normal characteristic of the growth cycle.

Two features were of special interest to Bernard, one, the invariable infection of roots as compared with the complete immunity shown by tubers; the other, the regular annual periodicity exhibited in respect to fungus infection. During August and September there is active vegetative growth without infection; from October, following the invasion of the roots by mycelium from the soil, to June, there ensues a period of tuberisation. In Bernard's view the two series of phenomena are causally related, i.e. fungal infection produces a general "intoxication" of the tissues made manifest, in the embryo, by the formation of the primary tubercle, in the adult plant, by the annual tuberisation of one or more of the axillary buds subsequent to root infection. In short, a brief phase of growth and differentiation

with freedom from infection alternates regularly with a longer period of tuberisation following root infection.

Later, Bernard showed that non-infection of the tubers was due to a fungicidal action exerted by the tissues (see *N.P.* 25, p. 93); he also demonstrated experimentally by his work on *Bletilla* that tuberisation of uninfected embryos could be brought about by raising the concentration of the substrate. Thus, seeds of this Orchid sown in aseptic culture developed slowly to plantlets with slender stems bearing leaves separated by distinct internodes, whereas, seeds germinated with an active strain of the endophyte showed rapid infection of the embryo followed by vigorous development, the resulting seedlings exhibiting marked differences in habit as compared with those lacking infection, e.g. they produced relatively massive axes with short stout internodes and crowded leaves of much larger size than those of uninfected seedlings. The tuberous base of the stem, at first covered by absorbing hairs, soon produced roots; as in the Ophrydeae, the latter suffered infection from the soil, while the swollen stem and protocorm remained free from infection.

Can this theory of tuberisation be applied to Flowering Plants generally? In seeking the answer to this question Bernard extended his observations to plants other than Orchids, e.g. to *Ranunculus ficaria* and the cultivated Potato (*Solanum tuberosum*). In the former, he thought the evidence was confirmatory of a relation similar to that which he believed existed in *Ophrys* and allied Orchids; in Potato, the observed facts were more difficult to explain.

It is well known that healthy potato tubers are free from infection by micro-organisms of any kind. Bernard's observations confirmed this and showed that the roots suffered infection of an irregular and apparently casual kind. Subsequently a fungus, believed to possess affinities with the genus *Mucor*, was isolated from the roots of *Solanum dulcamara*, a common British and European species of the same genus as Potato. At this stage the work was interrupted by Bernard's untimely death, and the identity of the fungus with that endophytic in the roots of the latter was left in doubt.

The investigation has since been resumed by his colleagues at the Pasteur Institute, who have extended the scope of the enquiry and repeated some of Bernard's later experiments. In a recent memoir Magrou (1921) has restated the theory of tuberisation just outlined and marshalled the evidence accumulated by Bernard and his successors. The observations on Potato are of particular interest.

Assuming that the ordinary relation between root infection and

tuberisation in the Potato has been replaced by effects due to cultivation, Magrou examined *S. maglia*, a wild Chilean species believed to be a direct descendant of the original ancestor of the cultivated Potato, and also *S. dulcamara*, the Bittersweet. In both species, the observed existence of mycorrhiza was thought to provide confirmatory evidence of a direct relation between infection and tuberisation. The irregularity of infection observed in the cultivated Potato is explained by assuming that the stimulus originally associated with fungus infection has been replaced by others depending upon high cultivation and manuring, "selection" having co-operated to preserve only the individuals which respond in this way. In support of this view, an appeal is made to records made in France in the eighteenth century by Parmentier, who is reported to have observed whole fields of potatoes without tubers, and to the occasional appearance on non-tuberizing individuals in ordinary crops. It must be noted, however, that an equally good explanation of this phenomenon of "zero-cropping" has been offered on genetical grounds by Salaman (1924) who interprets the absence of tubers as due to the presence of "inhibiting factors" in the genetical constitution of individual Potato plants or strains.

Owing to the scanty and irregular appearance of mycelium in the roots of cultivated Potatoes, *Solanum dulcamara* was used as a source of infection, in Magrou's experiments. Potato seed sown on poor soil from a station occupied by *S. dulcamara* gave seedlings which grew slowly but developed roots with typical endophytic infection. Evidence is offered that two distinct types of plants appeared in these cultures; those in which fungus infection takes place from the soil but the endophytic mycelium undergoes immediate and complete digestion and those in which infection persists giving rise to characteristic endophytic mycorrhiza. Plants of the former type possess "immunity" and consequently do not tuberise; those of the other type develop an abundant crop of tubers (Fig. 54).

Confirmation of the correctness of this interpretation can be provided only by synthetic experiments with "pure cultures" of the organisms concerned. Up to the present, experiments of this kind with Potato have not yielded perfectly satisfactory results. A fungus resembling that described by Bernard was isolated by Magrou from *S. dulcamara* and named *Mucor solani*. This form causes typical infestation of roots of Potato seedlings raised from sterilised seed and is believed by Magrou to be identical with, or closely related to, the original endophyte of the ancestral species.

It has, however, not yet been found possible to provide vigorous proof of a direct relation between root infection and tuber formation by means of strictly aseptic cultures as in the Orchids and *Calluna*, and a final expression of opinion must await the confirmatory evidence supplied by such cultures.

The work on Potato has been supplemented by observations on other plants: two species of *Orobus*, *O. tuberosus*, a perennial species with tuberous rhizomes, and *O. coccineus*, an annual species without a perennating shoot system; *Mercurialis perennis*, the Dog's Mercury, with an elaborate system of rhizomes, and *M. annua*, an annual herb with aerial shoots only. In both species of *Orobus*, infestation of the roots occurs; in *O. tuberosus* it persists as mycorrhiza; in *O. coccineus* the invading mycelium undergoes immediate destruction by the root-cells of the host, i.e. the symbiotic relation is not established and the annual habit persists. In the two species of *Mercurialis* named a similar state of things is reported and figured. In both genera, the difference in habit is believed to be associated with the higher "immunity" possessed by that species in which the mycorrhizal relation is not established (Fig. 54).

Taking into account his own observations, Laurent's demonstration that tuberisation can be provoked by raising the concentration of sugar in the culture medium, and Bernard's experiments proving that in pure culture the Orchid endophytes bring about a rise in the osmotic pressure of the substratum, Magrou considers there is good presumptive evidence for believing that, in some cases at least, the immediate cause of tuberisation is an increased osmotic pressure in the root tissues due to their invasion by endophytic fungi. Magrou's conclusions have been challenged by Peyronel (1924), who states that in Italy, *Mercurialis annua* frequently develops typical and persistent mycorrhiza, while on the other hand, many perennial herbaceous species are entirely free from it (Peyronel 1924).

In its extended form, the theory of tuberisation outlined in this chapter has been accepted by Constantin (1922), whose conclusions have been summarised as follows: "The association of perennial species of plants with soil fungi has brought about a permanent symbiosis—a condition which does not occur with annual species. Since the perennial character in plants is due to the low temperatures of high altitudes and latitudes, cool climates may be considered as favourable to the establishment of symbiosis. Cultivated Potatoes have lost the mycorrhizal relations of the primitive forms to which

tuberisation was due and in order to produce tubers without this relationship they must be grown in cool climates" (Constantin, 1924). More than one controversial issue is raised in this passage, but space does not now permit their further discussion.

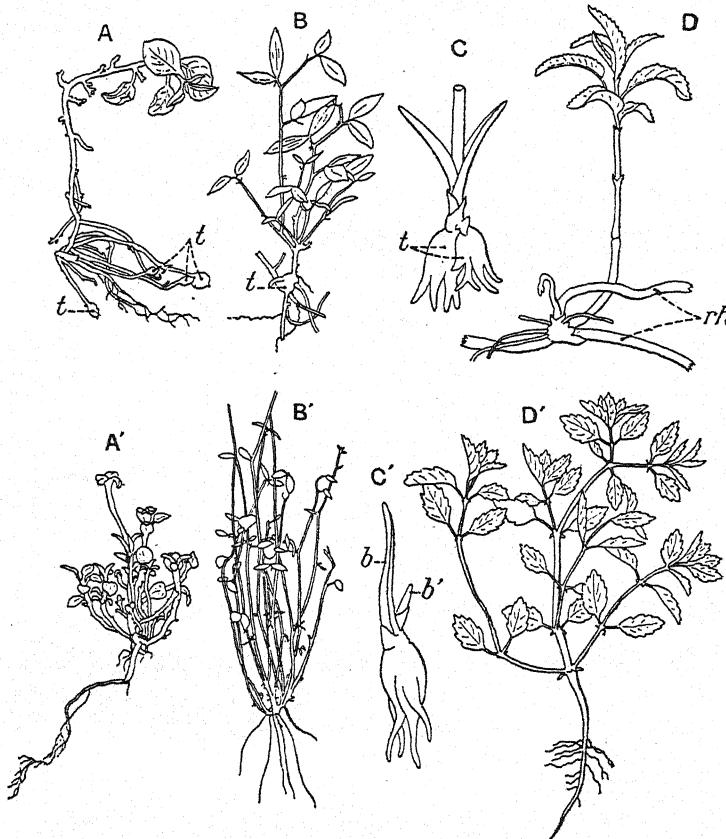


FIG. 64. Dimorphism and symbiosis. A—D, plants which have suffered infection and formed mycorrhiza; A'—D', plants which have suffered infection, but, owing to rapid digestion of mycelium by the root cells, have not formed mycorrhiza. A, A', *Solanum tuberosum*; B, B', *Orobis tuberosus*; C, C', *Orchis maculata*; D, *Mercurialis perennis*; D', *Mercurialis annua*. t, tubercles; rh, rhizomes; b (fig. C'), main axis of *Orchis maculata*; b', secondary axis developing to a shoot. C and C' after Noël Bernard.

(From Magrou, *Ann. d. Sci. Nat.* 1921.)

In conclusion, while recognising the extremely suggestive character of the facts presented by Magrou, it appears somewhat doubtful whether sufficient positive evidence has yet been accumulated to

serve as a sure foundation for the imposing superstructure raised upon it. In particular, crucial evidence respecting the behaviour of Potato plants with and without infection in aseptic cultures would be welcomed, as also would be an extension of the comparative observations on *Mercurialis* and corresponding types to plants from as many and varied stations as possible. In its present form this stimulating theory of the cause of tuberisation and the origin of the perennial habit should serve as a valuable incentive to further researches in this fascinating field of work.

CHAPTER XI

The physiological significance of mycorrhiza and the nutrition of mycorrhiza plants—Critical review of evidence derived from researches on forest trees, orchids and heaths—Endotrophic infection in other species—Summary and conclusions.

WHAT is the real significance of mycorrhiza and the mycorrhizal habit? It is more than half a century since Frank first asked this question, coining a new name to mark the recognition of root infection by fungi as a normal and regular phenomenon in vascular plants. Of necessity much of the earlier work was descriptive and analytical rather than experimental. The problem bristled with difficulties, some of them very imperfectly understood, and many of the earlier experiments designed to throw light on the biology of the association failed in their object, partly by reason of the prevailing ignorance respecting soil conditions, partly from lack of a suitable technique for isolating the endophytes and establishing their identity. It was not until Bernard applied the methods of the bacteriological laboratory to the study of Orchid mycorrhiza that any real advance was made, and it is now fully recognised by all competent workers at the subject that further knowledge can be gained only by the use of similar methods.

Investigations of the kind indicated are apt to be laborious and they involve the application of a special technique. The isolation of the specific endophytes, their maintenance in pure culture, and the synthesis of fungus and vascular plant under pure culture conditions, all present difficulties. Moreover, evidence of behaviour under rigid experimental control of this kind must be applied with great caution to conditions in nature. Thus it is that the bionomics of mycorrhiza and the nutrition of mycotrophic plants are still, in large measure, the subjects of controversy, although enough is known to correlate

them with kindred phenomena of parasitism and the parasitic habit, and to bring them into close touch with the problems presented to the forester and the student of plant ecology in the field.

The present occasion offers a suitable opportunity to review the experimental evidence available and to learn, incidentally, how far it provides support for the more or less speculative theories of nutrition put forward by earlier observers. Two aspects of the problem must receive attention, one relating to green species autotrophic in respect to their carbon nutrition, the other to the non-green forms usually regarded as saprophytic.

Excepting parasites and insectivorous plants, the habit is known to be widespread among terrestrial species, affecting a very large number of families and intensively developed in a certain number of them. Mycorrhiza is found in epiphytes although usually absent from the aerial roots, and, with a single exception, is invariably well developed in non-chlorophyllous "saprophytes," e.g. *Neottia*, *Corallorrhiza*, *Monotropa* and its allies. *Wullschlaegia aphylla*, an Orchid reported by Johow (1889) to be entirely free from fungus infection, is unique in this respect and requires reinvestigation.

Although modern work has not confirmed the view that the ectotrophic and endotrophic habits can be sharply distinguished from one another, it is still convenient to classify mycorrhizas in two main groups, the extreme types of which show marked structural differences, associated with the distribution and character of infection. In one, a more or less extensive distribution of intracellular mycelium is associated with a variable development of hyphae on the outside of the root; in the other, specially characteristic of trees and shrubs, a sheath of mycelium is formed about the tip and younger part of the root and the mycelium comprising the mantle is continuous with an intercellular net of hyphae in the outer cortex. Intercellular infection, formerly believed to be restricted to the epidermis, has been reported in the cortical tissues of many mycorrhizas of the latter type, so giving rise to the intermediate type of structure named *ectendotrophic*. With few exceptions, the ectotrophic (including the ectendotrophic) habit is limited to woodland soils and its appearance is possibly related to a special environment rather than to any fundamental distinction of a biological kind.

There is no need to labour the point that every possible opinion has been held respecting the physiological relations in mycorrhiza. The nature of these views has been sufficiently indicated in the preceding pages, and it would be tedious to recapitulate the arguments

put forward in their support. In the sense intended by de Bary, the relationship is clearly one of *symbiosis*, and the constituents may correctly be described as *symbionts* without any implication that their mutual relation is advantageous or the reverse.

Are the endophytic fungi parasites of a relatively harmless kind or is there a reciprocal relation beneficial to either symbiont or to both?

Two general observations provide evidence of an indirect kind in support of the last-named view. Firstly, it is the young and actively absorbing roots which become mycorrhizas; secondly, there is no cytological evidence of damage to the living constituents of invaded cells. Direct evidence bearing on the enquiry may be derived from three independent sources; namely, the results of experimental investigations on forest trees, Orchids and Heaths respectively.

The mycorrhiza of trees. Melin's work on conifers and deciduous trees has been fully reviewed in an earlier chapter. Certain facts may be regarded as well established. In Sweden a number of Hyphomycetes have been identified as endophytes of Pine and other trees. These forms belong to saprophytic genera, the fruit bodies of which are a constant feature of the woodlands concerned; there is no evidence of parasitism of the ordinary kind nor do they belong to parasitic genera. The ectendotrophic rather than the ectotrophic habit prevails, but such mycelium as becomes intracellular undergoes rapid digestion in the cortical cells. It is likely that some at least of these fungi are obligate symbionts, unable to reach their full development except in association with the roots of their hosts; on the other hand, there is at present no evidence that the early stages of seedling development in any tree is bound up with fungus infection. Pure culture experiments have yielded abundant evidence of specialisation on the part of these root fungi as compared with indifferent soil species. Grown apart from their hosts, they make relatively slow and feeble growth, and show marked sensitiveness to external conditions, e.g. to the hydrogen-ion concentration of the substratum and the character of the food material. Most significant is the observation that normal mycorrhiza is developed only in a suitable rooting medium: its formation is easily inhibited, for example, by a change in the reaction, by unsuitable nutrient, or by the presence of toxic substances such as are formed in humus by heat sterilisation. It is of particular interest to note that, under such adverse conditions, the roots are not subject to a more intense attack. On the contrary, the presence of factors unfavourable to fungus growth inhibits the formation of hyphal complexes in endotrophic mycorrhizas and

produces a corresponding reduction of infection in those of ectotrophic type. Under conditions inimical to growth of the seedling the association may lapse into parasitism, while in unfavourable soil conditions pseudomycorrhiza is formed as a consequence of invasion of the roots by soil fungi other than the true endophytes. In short, the formation of mycorrhiza by conifers is shown to be a reciprocal phenomenon conditioned by the physiological states of both symbionts, this in turn being correlated with external conditions of soil and climate. There is good evidence that the fungi profit from the association: they show a marked stimulation from contact with living roots, attributed to the presence of small quantities of exudates, in particular phosphatids, and there can be little doubt that they obtain carbohydrates, especially glucose, from their vascular hosts.

With respect to the absorption of mineral salts other than compounds of nitrogen, Melin carried out a special investigation, making ash estimations of seedlings grown with different combinations and concentrations of salts. He concluded that inorganic salts are taken up as efficiently by infected as by uninfected roots. In view of the relative poverty of free salts in the superficial layers of raw humus as compared with mild humus soils, he was led to the view that absorption of inorganic salts was probably carried on more effectively in the former by mycorrhiza than by uninfected roots—in short to a qualified agreement with the Stahl hypothesis in respect to this matter.

In respect of nitrogenous metabolism the experimental evidence accumulated by Melin is even more striking. In pure culture the endophytes have been found to utilise nucleic acid and like organic compounds much more efficiently than do the seedlings of their hosts. Accordingly, in synthetic cultures supplied with nucleic acid or peptone as sources of nitrogen, the roots of Pine seedlings possessing mycorrhizas do not develop the marked symptoms of nitrogen starvation displayed by those of seedlings grown alone (cf. Fig. 56). On the other hand, there is at present no evidence that any of the known root fungi of trees, whether alone or in association with their hosts, can assimilate free nitrogen.

A critical examination of the experimental evidence confirms the main conclusion reached by Melin, namely, that root infection by fungi possesses a vital significance for trees and plants growing in raw humus soils. In Northern Europe, tree mycorrhiza is typically developed under such conditions, and there is good reason for believing that the soil reaction and the character of the nitrogenous compounds present in the humus are important factors in main-

taining mycelium in a physiological condition favourable to its formation. The supply of nitrates is very deficient in these woodland soils. Conifers, and in all probability other trees, can utilise ammonium compounds and possibly to some slight extent, more complex organic compounds of nitrogen, but the last named are much more readily used by the root fungi. Hence, on acid humus soils in which such compounds constitute the chief source of nitrogenous nutrient, plants provided with mycorrhiza are extraordinarily well equipped for competition with other soil organisms. Nutrient material assimilated by the mycelium, if soluble, can enter the root cells directly from the hyphae which invest them, if insoluble, a proportion becomes available by digestion of those hyphae which enter the cells. It is perfectly clear from the experimental evidence now available that the presence of an investing sheath of mycelium about the absorbing region of the roots offers no hindrance to the passage inwards of water and dissolved substances.

In so far as they have been experimentally proved, these conclusions apply only to certain coniferous trees. There can be little reasonable doubt of their ultimate extension to other conifers and also to deciduous trees growing under similar soil conditions and showing a similar mycorrhizal habit. Assuming that the mycorrhizal condition in other trees resembles that in the conifers studied by Melin, it is not possible to doubt the existence of a reciprocal relation conferring benefit upon the trees in certain types of soil by facilitating the intake of nitrogenous food material. While there is good evidence of an advanced degree of specialisation in respect to the symbiotic habit in certain of the endophytes, there is at present none pointing to the existence of an obligate relation or an advanced degree of dependence upon infection on the part of any host tree. In this connection it is perhaps significant that the loss of chlorophyll and the vegetative reduction associated with the saprophytic habit is not known among trees or shrubs, although it is well marked in woody parasites such as the Loranthaceae. The ectotrophic and ectendotrophic types of mycorrhizal structure so common in trees may be related in part to the saprophytic character of the fungi concerned, in part to the abundance of organic residues present in woodland soils.

The conclusions outlined above are supported by the results of Falck's researches on the nutritive significance of mycorrhiza in acid woodland soils ("Rohhumusboden"). (Falck 1923.)

Orchid mycorrhiza. What is the relation between the chlorophyllous Orchids and their root fungi? Does Bernard's conception

of it as one of parasitic attack, countered by a mechanism conferring a relative degree of immunity upon the host, cover all the known facts? That it has served to illuminate and explain many aspects of the problem there can be no doubt. Nevertheless, it does not and cannot provide an explanation of the two most characteristic features of the partnership; namely, the obligate character of the connection between infection and seedling development, and the association of specific strains of *Rhizoctonia* with individual Orchid species over wide geographical areas.

Notwithstanding the specialisation incidental to their symbiotic habit, the Orchid fungi appear to retain unimpaired the power of autonomous existence, thereby differing sharply from the root fungi of conifers. They are easily isolated, grow readily in many different media, and produce conidia and sclerotia when grown apart from their hosts. Burgeff reported that the formation of these structures in pure culture was bound up with the concentration of the medium and the amount of metabolite present. The effects of prolonged culture outside their hosts upon the capacity for inducing seedling development are still somewhat obscure and the observations of different workers are at variance.

With respect to nutrition, the salient facts have been described so often and by so many different observers that it is unnecessary to recapitulate them in detail. It can hardly be doubted that the condition observable in living Orchids has been evolved from one following upon invasion of the roots by facultative parasites. In general, the appearance of intracellular mycelium coincides with the disappearance of starch from the invaded cells, and Burgeff showed that in pure culture starch was hydrolysed by diastatic enzymes, the resulting maltose undergoing in certain cases further hydrolysis to glucose. Cane sugar was also removed from the medium, in part inverted, in part directly utilised by the mycelium; glucosides were hydrolysed with removal of the resulting sugars, and cytase and tyrosinase were identified in individual strains. The presence of proteolytic enzymes was likewise reported by the same author. Of nitrogenous nutrients, peptone and salep proved most acceptable, while ammonium compounds were preferred to nitrates. There can be no doubt that the "Eiweisshyphen" that suffer intracellular digestion in the tissues of Orchids contain much protein material, which presumably becomes available to the host cells. This conclusion is supported by the experimental observations of Fuchs and Ziegenspeck (1922) and of Wolff (1925, 1926) on *Neottia* (see *N.P.* 25, p. 107), although, in green Orchids, it is not certain what proportion of

it represents material filched from the root cells during the initial phase of fungus activity.

Burgeff found no evidence that any of the Orchid endophytes could utilise atmospheric nitrogen, yet in a preliminary communication H. Wolff (1925) reports nitrogen fixation for the endophyte of *Neottia* in pure culture and promises further information based on experiments now in progress. It is probable that the last word on this matter has yet to be said.

The outstanding difficulty in ascribing a beneficent rôle to the root endophytes of green Orchids lies in the fact that, while it is theoretically possible for the mycelium to draw upon food reserves locked up in soil humus, there is in most species but a scanty development of mycelium on the external surface of the roots. On the other hand, it is characteristic of Orchid mycorrhiza that infection does not spread throughout the plant body, but takes place intermittently from without. This, in itself, involves a recurrent "tapping" of the contents of hyphae in direct contact with the soil.

It is possible to regard the obligate relation as a temporary phase related definitely to the developmental stage of growth and dependent, as regards physiological mechanism, upon a rise in the concentration of osmotic substances in the cells of the embryo, but the evidence is still conflicting as to whether or not the mature plants of all Orchids can thrive in the absence of their root fungi. It is of interest to note that different Orchid genera respond differently to seed infection. For example, it was definitely put on record by Bernard that more favourable results were obtained with *Cattleya* seed by using the asymbiotic method of germination, e.g. in his experiments by raising the concentration of salep used in the medium. In the application of pure culture methods of germination to horticultural practice, cases have been recorded in which germination in the neighbourhood of 100 per cent. was secured with *Cattleya* seed, only after more than one strain of the endophyte had been isolated and tested. It is significant that Knudson bases many of his arguments on statements made by Bernard in reference to this genus, members of which often behave in an anomalous manner, as the latter clearly stated.

The successful application of asymbiotic methods to effect germination is not questioned, but they involve the provision of aseptic conditions that do not occur in nature, and are not found to be requisite in horticultural practice when the endophytes are supplied. Moreover, in certain genera, seed development and growth take place more rapidly in fungus-infected cultures than in those pro-

tected from infection (cf. Pl. III, Figs. 24, 25), and it is clear from the facts put on record by Clement (1922) that in asymbiotic seed cultures of certain genera the substrata must be very carefully adjusted to the needs of particular species (see *N.P.* 25, p. 106).

In the chlorophyllous Orchids, it is possible to postulate a beneficial effect upon the host in respect to the seedling only, while regarding the mycorrhizal relation in the adult as an incidental evil, combated and held in check by a relatively efficient mechanism of resistance. The occurrence of a number of non-chlorophyllous species in itself raises doubts as to the correctness of this interpretation, and favours the view that the endophytes play an important part in the nutrition of all Orchids. It is tempting to regard the non-chlorophyllous forms as the end terms of a series culminating in complete dependence upon the fungal symbionts. Excluding the possibility of nitrogen fixation by the vascular partners, for which there is no evidence whatever, these species must obtain the whole of their nutrients from the soil, i.e. all the carbonaceous, and the larger part of the nitrogenous materials required must be presented in the form of humus constituents. There are, accordingly, but two possible alternatives in respect to nutrition; either the higher plants can themselves deal directly with the insoluble humus compounds available, or they must obtain the requisite supplies second-hand as a result of the activities of the intracellular mycelium with which the roots are so lavishly supplied. There is no experimental evidence in favour of the former hypothesis, and the provision of such evidence involves the raising of plants free from infection, and their maintenance in aseptic cultures; the alternative view has usually been assumed, and all the arguments applied to its support in the case of green species acquire an added force in that of the non-green forms. The corollary of this tentative conclusion has not received the attention it deserves, namely, that the non-chlorophyllous Orchids are not "saprophytic" but are, in the main, parasites upon their endophytic fungi. It may be observed that all these plants are characteristic members of the vegetations of woodland humus. It follows, therefore, that the benefits conferred upon the vascular hosts in organic soils are common to both ecto- and endotrophic types of mycorrhiza, since *Monotropa* and its allies closely resemble *Neottia* and similar Orchids in respect to the reduction and loss of vegetative features associated directly with the autotrophic habit. The opinion is thus confirmed that the extreme types of structure known as ectotrophic and endotrophic respectively have a similar significance

in respect to nutrition, although curiosity is whetted once more as to the details of the physiological mechanism responsible for this result.

In *Gastrodia* there can be little doubt that this is actually the case. For the remainder of this relatively large and extremely interesting group, there is, as yet, no direct experimental proof. The case of *Wulsschlaeglia* acquires critical importance in this connection; in view of the improvement in technique since Johow's observations were made, it requires to be reinvestigated.

There is at present a notable lack of comparative data in respect to seed germination in non-chlorophyllous Orchids. In *Neottia* the earlier stages of development were studied by Bernard (1899)¹. The endophyte is a form included in *Rhizoctonia repens* Bernard, and the details of infection resemble those noted in other genera save in respect to the heavier infection and wider distribution of mycelium observed in *Neottia*. It would be of particular interest to study the behaviour of seeds of *Neottia* and other species lacking chlorophyll under asymbiotic conditions, to ascertain whether the stimulus normally exerted by the endophytes can be replaced by the addition of organic substances to the substratum, and if so, estimate the capacity of the resulting seedlings to assimilate organic nutrients in the absence of mycelium.

The remarkable case of *Gastrodia* (Kusano, 1911) also challenges attention as one in which an association with a fungus of the *Rhizoctonia* type apparently does not occur and for which there is at present no information respecting seed germination or the earlier stages of seedling development.

It was in Orchids that infestation of the roots by fungus mycelium was first clearly recognised. In spite of the relatively exact knowledge that has been acquired, there remains still much that is puzzling in the relation of fungus and host in this group of plants. In the evolutionary sense, it must have originated in parasitic attack on the part of certain soil fungi adequately combated and held in check by the victims. This view assumes the existence of relatively benign strains of the attacking fungus, or of individual Orchid plants possessing relatively high resistance to parasitic invasion of the roots. In species frequenting humus soils and in epiphytes, root infection may have resulted in the "tapping" of organic residues otherwise inaccessible, and undoubtedly this would be facilitated by the

¹ "J'ai eu la bonne fortune de trouver, dans la Nature, des milliers de graines en germination d'une Orchidée indigène (*Neottia Nidus-avis*)."
(Bernard 1902.)

intermittent character of infection. In those Orchid species specially associated with chalky and limestone soils, it is unlikely that this source could yield food supplies of any significance.

The obligate relation is clearly secondary: it is nutritive in origin and probably affects only the early stages of development; confirmatory evidence is required that it persists in the adult plant.

The mycorrhiza of Heaths. Turning to Ericaceae, another group for which critical results are available, it may be noted that while an obligate association with specific endophytes is common to Orchids and Heaths, the structural features of the mycorrhiza in plants belonging to the latter group resemble those in conifers rather than in Orchids. The incidence of infection in the tissues is more superficial, and there is a more profuse development of mycelium on the surface of the roots. In *Calluna*, there is a tendency for hyphae to accumulate about the root tips, and in other genera, e.g. *Vaccinium* and *Arbutus*, the younger part of the roots may be invested by a complete sheath of mycelium—the tuberous mycorrhiza of *Arbutus unedo*, for example, is typically ectendotrophic in structure.

Now *Calluna* and many of its allies are characteristic and abundant members of the vegetation of humus soils—moorland, heath, and woodland—a notable feature of such soils being a deficiency of mineral salts, especially nitrates. Under field conditions, the intensity of infection in *Calluna* varies. As observed by the writer, mycorrhiza is profusely developed in soils with abundant humus: on peaty heaths and moorlands, and in cultivated garden soils. It is more sparsely formed in dry sandy situations, where, at certain times of the year, its roots although infected may appear to be free from mycelium. In experimental cultures this immunity from infection may be even more striking. Thus, it is now believed by the writer that *functional* mycorrhiza is not formed in aseptic cultures, whether sand or agar-agar, supplied with inorganic nutrient solutions, or in peat sterilised by heat, the latter being temporarily extremely toxic as a rooting medium. Cytological observations, as yet incomplete (see p. 109), indicate that a marked change in the metabolic processes leading to the appearance of fats in the root cells, coincides with suppression or reduction of the usual hyphal complexes. The significance of such changes in relation to nutrition has not yet been investigated.

These fluctuations are similar in kind to those observed in conifers, and they appear to be correlated with corresponding differences in the rooting medium, i.e. in nature, variation in the

amount and character of the organic constituents; under experimental conditions, the absence of organic compounds or the presence of toxic substances such as those produced by heat sterilisation.

Hence, in *Calluna* as in conifers, the production of healthy and functional mycorrhiza seems to be directly related to the presence of factors favourable to the growth of the mycorrhizal fungi, in effect, to soil conditions not readily reproduced under "pure culture" conditions.

A case for exchange of nutrient material with a balance of profit on the side of the vascular plant has been set out, and the opinion expressed that in *Calluna*, the endophyte operates as an internal factor of a special kind directly related to the metabolism of the root cells in certain kinds of soil. Evidence has been supplied that the formation of mycorrhiza is "a reciprocal phenomenon, conditioned not only by the activity of the fungus, but by the reaction of the root cells and the nature of the rooting medium" (Rayner, 1925).

In view of the reciprocity observed both in conifers and in *Calluna* between the constitution of the rooting medium and the character of infection, it seems probable that Melin's conclusions respecting the beneficial effects resulting from the presence of the mycorrhiza in acid humus may be extended to the more specialised case of *Calluna*. Under such conditions, the mycorrhiza of this species, and doubtless of other ericoids, probably functions in a similar way to that of trees, conferring on the host plant the power of drawing upon the organic food reserves locked up in humus. In Ericaceae, the relation is more specialised than in trees. In each species infection is restricted to a single endophyte showing a relatively high degree of specificity, and there is positive evidence for believing that the capacity for utilising organic compounds of nitrogen is supplemented by nitrogen fixation on the part of the endophytes (Rayner, 1922, 1925).

On this view the mycorrhizal habit in *Calluna* and its allies may be regarded as an attempt—as successful in its way, although attended by greater risks to the host, as that manifested in the tubercles of legumes and other nodule-forming species—to solve the problem of obtaining the requisite supplies of nitrogen on soils deficient in nitrates. Like certain conifers and other trees, *Calluna* and its allies are not strictly autotrophic in respect to their nitrogen metabolism, and they are singularly well equipped for successful competition in the struggle to obtain the requisite nitrogenous food materials, whether in sandy soils, poor in organic constituents, or in acid humus

soils deficient in nitrates. They have "solved the problem of growth upon the poorest and most unpromising soils, but they have solved it at the price of their independence" (Rayner, 1915).

Although infection by the appropriate endophyte is an obligate condition for seedling development in *Calluna* and other ericaceous species, there is no proof that the formation of typical mycorrhiza is essential to the mature plants, albeit there is good evidence that it renders available sources of nitrogen otherwise inaccessible. The exact nature of the benefit so gained may fluctuate with the edaphic character of the habitat; for example, nitrogen fixation may be in abeyance when organic compounds of nitrogen are abundant.

With regard to the exchange of organised food materials in mycorrhiza plants generally, McLennan has provided evidence that the root fungus of *Lolium* forms fats; in the later stage of growth the "sporangioles" become gorged with oily material transferred from the adjoining hyphae. The fat is ultimately discharged into the cells, where, presumably, it is hydrolysed, and whence it is translocated during the fruiting season of the host (Figs. 61, 62).

The cytology of the infected tissues in *Lolium* and *Gastrodia* has been compared. McLennan interprets the physiological relation in both species as a metabolic exchange "from the fungus to the higher plant, with the result that the latter obtains a supply of fat or oil" (McLennan, 1926).

The author lays special emphasis on the exchange of carbonaceous rather than nitrogenous food materials, as deduced from cytological features in *Gastrodia* and *Lolium*. But it must be noted that the former plant is likewise dependent upon the endophyte for the whole of its nutrient material, and there appears to be no reason to assume that in *Lolium* the translocations of fatty and nitrogenous food materials are alternative or mutually antagonistic processes. More reasonable is the view that the exact nature of the exchange in each case is intimately bound up with the metabolism of the particular host plant, with the stage in development, and possibly, in some cases, indirectly with edaphic peculiarities. A similar transference of fatty material from mycelium to root cells, followed by removal of the stainable material, takes place in the root cells of *Calluna* during digestion of the mycelial complex. It is believed that the fat metabolism of the latter plant, and presumably that of other ericaceous species, may have an important bearing on their nutritive relations with the endophytes, and also with their reaction to calcareous soils, and that a clearer understanding of it may throw

further light on the significance of the calcifuge habit in Ericaceae. It is hoped that work now in progress may render it possible to relate the two sets of phenomena more precisely.

Although members of the Monotropoideae have long attracted attention, no experimental data are yet available respecting germination, seedling development, or the real significance of the saprophytic habit in members of this group of Ericales. In view of the obligate relation in Heather and kindred species, it is tempting to regard them as the end terms of a series culminating in complete dependence upon their fungus associates. Whether or not this is actually the case, an experimental study of these interesting plants is long overdue. Unsuccessful attempts to germinate seed of *Monotropa hypopitys* have been made by more than one observer including the writer, and it is already certain that germination cannot be effected by the ordinary asymbiotic methods.

There is little experimental evidence bearing on the exact nature of the biological relation in mycorrhiza plants other than those included in the specialised groups just considered. The uniform type of infection, i.e. by mycelium bearing vesicles and arbuscules, and the prevalence of intracellular digestion favour the conclusions that the endophytes of many vascular plants belong to a single group, and that the physiology of the relation does not differ fundamentally from that in the cases studied experimentally. No satisfactory evidence exists that an endophyte of this type has yet been isolated, in itself an indication of specialisation to the symbiotic habit: nor is anything known about the bionomics of "double infection" as reported by Peyronel for many mycorrhizal plants that show primary infection by mycelium bearing vesicles and arbuscules. Save in respect to its mode of entry, the latter appears to behave as a saprophyte rather than as a parasite. Starch and possibly other metabolites are removed from the cells, although any benefit accruing to the fungus must be evanescent in view of the extensive digestion of mycelium which eventually takes place. It is possible that a beneficial effect upon the host may be related directly to soil conditions; for example, in soils rich in natural humus or heavily manured, the mycelium may bring in material derived from organic residues and so restore more than was originally removed from the root cells.

The condition in *Lolium*—more particularly in view of the possibility that the hyphae in root and shoot respectively belong to the

same fungus—together with the appearance of the "saprophytic" habit in certain families, e.g. Lycopodiaceae, Ophioglossaceae and Gentianaceae, suggests that a relatively advanced condition has already been evolved in certain groups. The physiology of the symbiotic relation doubtless varies from species to species—possibly from individual to individual. Only by experiments with infected and uninfected plants can final conclusions be reached as to the effects of infestation upon the hosts. In the relatively favourable conditions inseparable from pure culture experiments, it is not impossible that plants normally subject to mycorrhiza formation would thrive better protected from infection. Great caution is therefore required in applying results deduced from experimental cultures to plants growing in nature. Whereas under "sheltered" conditions, mycorrhiza formation may be incidental to seedling infection and of little significance in nutrition, it may become of critical importance to plants exposed to the full brunt of competition in the field.

In its evolutionary aspect the relation now existing in Orchids and Heaths must have originated in parasitism on the part of certain soil fungi. Assuming the existence of strains capable of invading living roots but relatively benign in their action and likewise the presence of individual hosts with a relatively high resistance to parasitic attack, it is not difficult to reconstruct the stages by which a symbiotic association was initiated. The endophytic habit brought with it certain changes in the metabolism of both partners, clues to the nature of which may be sought in the response shown by Orchid embryos to an increased concentration of sugar in the substratum, and in the still unknown mechanisms by which seedling development is activated in *Calluna* and other ericoids.

On any hypothesis, the evolution of an obligate relation with a parasitic or facultatively parasitic fungus is difficult to explain, and raises question of profound interest to students of heredity. Both in the Orchids and in *Calluna* it is associated now with an early stage of seedling development and in neither case is there satisfactory proof that it persists in the adult. From the reaction of Orchid embryos towards increased content of sugar or other organic nutrients in the substratum, it may be surmised that the association is intimately bound up with metabolic changes induced by the presence of the endophyte in the tissues.

The mycorrhizal habit in trees appears to have had a somewhat different origin and to have evolved along rather different lines.

Originating in the attraction exerted on saprophytic soil fungi by the presence of exudates—especially phosphatids—about the growing roots, it seems possible that the ectotrophic habit resulted from the feebly parasitic character of the fungi present, and that this structure in its purest form represents an early stage in the evolution of tree mycorrhiza. With the symbiotic habit thus established came in time a more efficient mechanism for penetrating the root tissues, the extension of intercellular infection to the more deeply placed root tissues and the appearance of the ectendotrophic type of structure. There is in trees no evidence of an obligate relation with seedling development and the formation of typical mycorrhiza appears to be bound up with the utilisation of the organic residues in humus. Producing comparatively small effects under the sheltered conditions inseparable from experimental culture, the presence of active mycorrhiza may have become a critical factor in nature, determining the survival value of the host trees in the competitive struggle for the available nutrients in humus and woodlands soils. Viewed from this angle the comparative observations of Möller and others, on the condition of roots in respect to infection in soils of differing character, acquire an added significance and find their place in the theory of nutrition put forward recently by Melin.

It is well to recall the fact that in the plant world, the severity of the struggle for existence not uncommonly centres about the competition for suitable compounds of nitrogen. Many of the most striking "adaptations" known are directly related to it, e.g. the insectivorous habit, and the formation of root nodules as a reaction to invasion of the tissues by nitrogen-fixing bacteria. Even the rôle of vascular plants in general as "nitrate organisms" may be so regarded, forming, as it does, an indispensable link in that remarkable cycle of chemical changes by which the "circulation of nitrogen" is secured and maintained in nature. On *a priori* grounds, it is not unreasonable to believe that the intimate association with fungus mycelium, so common in all groups of vascular plants and also in the thalloid members of Bryophyta, is but another manifestation of the urgency of this nitrogen problem among plants. In at least two of the three groups of mycorrhizal plants for which experimental data are now available, namely, forest trees and members of Ericaceae, modern work has yielded corroborative evidence that this is actually the case.

For Orchids, the evidence in support of this general hypothesis is less convincing, although there can be no doubt that nitrogenous

substances are present in rich abundance in the "Eiweisshyphen" which constitute so conspicuous a feature of the intracellular mycelium within the root tissues.

How the root fungi can derive any but a very temporary benefit from the association is not evident. In the case of tree mycorrhiza, Melin's researches lead him to postulate the existence of a large group of fungi belonging to the Hymenomycetes which cannot rightly be described as either parasites or saprophytes. Physiologically, they stand in closer relation to parasites and it is suggested they should be known as *Symbiophiles*.

The endophytes of Orchids and Heaths have definite affinities with parasitic forms and the primary relation with their vascular hosts must undoubtedly have been one of "attack and defence" as postulated by Bernard. From this has been evolved a condition of equilibrium, relatively stable in character although easily disturbed by changes in the environment, with the balance of profit—certainly in *Calluna* and allied species and probably also in Orchids—definitely on the side of the vascular partners.

Specialisation has been accompanied by physiological changes affecting the metabolism of both partners, notably in regard to the appearance of an obligate relation of a temporary kind in the early stages of seedling development. The origin and precise significance of the latter are at present obscure; it may be possible to relate it, on the one hand with metabolic changes associated with the endophytic habit, on the other with the saprophytic mode of nutrition normal to the embryo stages of seedling development.

What bearing have these conclusions on the theories of nutrition put forward by the earlier workers? Allusion has been made to the views expressed by Hartig and others respecting parasitism on the part of the root fungi of trees. Melin's conclusions, on the contrary, support the theory of beneficial symbiosis first put forward and maintained by Frank and his school. Is it possible to reconcile these divergent opinions? Is it, for instance, worth enquiring whether there is any evidence that the equilibrium implied in the existence of a symbiosis beneficial to the trees is ever disturbed in nature? Under experimental conditions such disturbance has been noted with resulting injury to the hosts. It has not been actually observed in the field, but Melin has expressed the opinion that overthrow of the "balance of power" ordinarily maintained, may easily occur during the earlier stages of growth. If seedlings are feeble or the mycelium too vigorous, there is a tendency for the root fungi to

become parasitic; if the young trees are healthy and the mycelium well nourished, equilibrium is established and maintained and the relation may fairly be described as *mutualism*.

On the whole it may be said that the views so strongly held by Frank, Stahl and their followers have survived the test of experimental enquiry. The arguments employed are not always acceptable in the light of modern research, but, in the opinion of the writer, there can be no doubt that recent investigations by means of pure cultures have tended to support the view that the possession of mycorrhiza is frequently of benefit to the vascular hosts, the nature and extent of such benefit depending upon the physical conditions of the environment and the physiology of the association in individual cases.

(Concluded)

SOME FLOWERS AND THEIR DIPTERAN VISITORS

BY E. AND H. DRABBLE

IN 1917 a list was published of the Syrphids which had been observed on a number of flowers¹. Since then we have extended our observations to other flowers and to all the families of the Diptera. Every species taken by us on flowers of the following plants has been identified, with the result that we are now able to record 124 species as visitors to 35 flowers.

A. Flowers with nectaries freely exposed:

Potentilla reptans L., *Rubus fruticosus* (agg.), *Angelica sylvestris* L., *Heracleum Sphondylium* L., *Chaerophyllum temulum* L., *Cornus sanguinea* L., *Sambucus nigra* L.

B. Flowers with nectaries concealed by scales:

Ranunculus acris L., *R. repens* L., *R. Flammula* L., *R. Ficaria* L.

C. Flowers with nectaries concealed by bases of stamens:

Convolvulus arvensis L.

D. Flowers with nectaries concealed within the corolla.

Alliaria officinalis Andrz., *Galium verum* L., *Scabiosa Succisa* L., *Matricaria inodora* L., *Chrysanthemum Leucanthemum* L., *Senecio Jacobaea* L., *Centaurea nigra* L., *Cnicus arvensis* Robs., *Lapsana communis* L., *Hypochaeris radicata* L., *Leontodon autumnale* L., *Taraxacum officinale* Weber, *Crepis capillaris* Wallr. (*C. virens* L.), *Hieracium boreale* Fr., *Euphrasia borealis* Towns., *Veronica Beccabunga* L., *V. Chamaedrys* L., *Mentha arvensis* L., *Stachys sylvatica* L.

E. Flowers without nectar:

Rosa canina L., *R. arvensis* Huds., *Phleum pratense* L., *Dactylis glomerata* L.

The Diptera observed on these flowers are given in the following lists. The number of species is indicated after the name of the plant.

A. Flowers with exposed nectaries:

***Potentilla reptans* L. (2).**

Melanostoma mellinum L.

Syritta pipiens L.

¹ E. and H. Drabble, The Syrphid Visitors to Certain Flowers, *New Phytologist*, 16, pp. 105-109.

Rubus fruticosus (agg.). (42).

The segregates of *R. fruticosus* are not listed separately as no marked differences were shown in their attractiveness for the Diptera.

Pipizella flavitarsis Mg.	Syrphus luniger Mg.
Chilosia variabilis Pz.	S. balteatus Deg.
Platychirus manicatus Mg.	S. cinctellus Ztt.
P. peltatus Mg.	S. auricollis Mg.
P. scutatus Mg.	S. labiatarum Verr.
P. albimanus F.	Sphaerophoria scripta L.
P. clypeatus Mg.	S. menthastris L.
P. angustatus Ztt.	Baccha elongata F.
Melanostoma mellinum L.	Ascia podagraria F.
M. scalare F.	Rhingia campestris Mg.
Leucozona leucorum L.	Volucella pellucens L.
Catabomba pyrastri L.	Eristalis tenax L.
Syrphus albostriatus Fln.	E. intricarius L.
S. tricinctus Fln.	E. arbustorum L.
S. lunulatus Mg.	E. pertinax Scop.
S. lineola Ztt.	Myatropa florea L.
S. vittiger Ztt.	Helophilus pendulus L.
S. grossulariae Mg.	Xylota segnis L.
S. ribesii L.	Syritta pipiens L.
S. vitripennis Mg.	Bucentes geniculata Deg.
S. latifasciatus Mcq.	Mydaea (Spilogaster) duplicita Mg.

Angelica sylvestris L. (9).

Ocydromia glabricula Fln.	Syrphus cinctellus Ztt.
Chrysogaster solstitialis Fln.	Eristalis arbustorum L.
Syrphus grossulariae Mg.	E. pertinax Scop.
S. ribesii L.	Sapromyza rorida Fln.
S. vitripennis Mg.	

Heracleum Sphondylium L. (80).

Rhamphomyia flava Fln.	Syrphus lineola Ztt.
Empis trigramma Mg.	S. vittiger Ztt.
Chrysogaster solstitialis Fln.	S. grossulariae Mg.
Chilosia scutellata Fln.	S. ribesii L.
Ch. variabilis Pz.	S. vitripennis Mg.
Ch. vulpina Mg.	S. corollae F.
Ch. illustrata Harr.	S. luniger Mg.
Ch. impressa Lw.	S. balteatus Deg.
Ch. albitarsis Mg.	S. cinctellus Ztt.
Ch. vernalis Fln.	S. auricollis Mg.
Ch. proxima Ztt.	S. umbellatarum F.
Ch. cynocephala Lw.	S. compositarum Verr.
Ch. carbonaria Lw.	Sphaerophoria scripta L.
Platychirus manicatus Mg.	S. menthastris Mg.
P. peltatus Mg.	Baccha elongata F.
P. scutatus Mg.	Rhingia campestris Mg.
P. albimanus F.	Eristalis tenax L.
P. clypeatus Mg.	E. arbustorum L.
Melanostoma mellinum L.	Eristalis pertinax Scop.
M. scalare F.	E. nemorum L.
Ischyrosyrphus glaucius L.	Myatropa florea L.
I. laternarius Müller	Xylota sylvarum L.

Syritta pipiens L.
Sericomyia borealis Fln.
Conops flavipes L.
Somalia simplicitarsis (rebaptizata
 Rnd.)
Eriothrix rufomaculata Deg.
Bucentes geniculata Deg.
Onesia sepulchralis L.
Sarcophaga carnaria L.
S. albiceps Mg.
S. atropos Mg.
Graphomyia maculata Scop.
Stomoxyx calcitrans L.
Morellia simplex Lw.
Mesembrina meridiana L.
Calliphora erythrocephala Mg.
C. vomitoria L.
Cryptolucilia cornicina F.
C. caesarion Mg.

Cryptolucilia sericata Mg.
C. illustris Mg.
Poliates lardaria F.
P. albolineata Fln.
Phaonia pallida F.
Mydaea (Spilogaster) duplicata Mg.
Hydrotaea irritans Fln.
Pogonomyia alpicola Rud.
Hylemyia variata Fln.
H. strigosa F.
Chortophila (Paregle) radicum L.
Ch. (P.) aestiva Mg.
Homolomyia verrallii Stein
Azelia macquarti Staeg.
Scatophaga squalida Mg.
Sapromyza decempunctata Fln.
Pelethophila florum F.
Trineura velutina Mg.

***Chaerophyllum temulum* L. (8).**

Melanostoma mellinum L.
Melanota volvulus F.
Somalia simplicitarsis (rebaptizata
 Rnd.)
Eriothrix rufomaculata Deg.

Mydaea (Spilogaster) leucorum Fln.
Hylemyia strigosa F.
H. fugax Mg. (*Phorbia pudica* Rnd.)
Chortophila (Paregle) radicum L.

***Cornus sanguinea* L. (4).**

Syrphus bifasciatus F.
Eristalis nemorum L.

Eristalis intricarius L.
Syritta pipiens L.

***Sambucus nigra* L. (1).**

Syritta pipiens L.

B. Flowers with nectaries concealed by scales.

***Ranunculus acris* L., *R. repens* L., *R. Flammula* L. (20).**

Liogaster metallina F.
Chrysogaster hirtella Lw.
Ch. macquarti Lw.
Chilosia barbata Lw.
Ch. intonsa Lw.
Ch. vernalis Fln.
Ch. albitarsis Mg.
Ch. impressa Lw.
Ch. proxima Ztt.
Ch. cynocephala Lw.
Platychirus manicatus Mg.

Platychirus albimanus F.
Melanostoma mellinum L.
Syrphus lunulatus Mg.
S. balteatus Deg.
S. auricollis Mg.
Syritta pipiens L.
Chrysochlamys cuprea Scop.
Chortophila (Paregle) radicum L.
Hylemyia fugax Mg. (*Phorbia pudica*
 Rnd.)

***Ranunculus Ficaria* L. (4).**

Bibio johannis L.
Chilosia pulchripes Lw. var. *fioccosa*
 Verrall

Chilosia nebulosa Verr.
Chortophila trapezina Ztt.

C. Flowers with nectaries concealed by bases of stamens.

Convolvulus arvensis L. (14).

<i>Chilosia barbata</i> Lw.	<i>Syrphus vitripennis</i> Mg.
<i>Ch. intonsa</i> Lw.	<i>S. balteatus</i> Deg.
<i>Ch. cynocephala</i> Lw.	<i>Sphaerophoria flavicauda</i> Ztt.
<i>Ch. impressa</i> Lw.	<i>Buccentes geniculata</i> Deg.
<i>Platychirus manicatus</i> Mg.	<i>Cryptolucilia cornicina</i> F.
<i>P. albimanus</i> F.	<i>Phorbia ignota</i> Rnd.
<i>Melanostoma mellinum</i> L.	

D. Flowers with nectaries concealed within the corolla.

Alliaria officinalis Andrz. (2).

<i>Melanostoma mellinum</i> L.	<i>Ascia podagraria</i> F.
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Galium verum L. (1).

<i>Melanostoma mellinum</i> L.

Scabiosa Succisa L. (5).

<i>Melanostoma mellinum</i> L.	<i>Volucella pellucens</i> L.
<i>M. scalare</i> F.	<i>Eristalis intricarius</i> L.
<i>Syrphus balteatus</i> Deg.	

Matricaria inodora L. (1).

<i>Syrphus corollae</i> F.

Chrysanthemum Leucanthemum L. (2).

<i>Chilosia pulchripes</i> Lw.	<i>Eristalis arbustorum</i> L.
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Senecio Jacobaea L. (7).

<i>Platychirus albimanus</i> F.	<i>Sphaerophoria scripta</i> L.
<i>Melanostoma mellinum</i> L.	<i>Eristalis arbustorum</i> L.
<i>Syrphus vitripennis</i> Mg.	<i>E. pertinax</i> Scop.
<i>S. balteatus</i> Deg.	

Centaurea nigra L. (13).

<i>Melanostoma mellinum</i> L.	<i>Rhingia rostrata</i> L.
<i>Catabomba pyrastri</i> L.	<i>Rh. campestris</i> Mg.
<i>Syrphus albostriatus</i> Fln.	<i>Volucella pellucens</i> L.
<i>S. ribesii</i> L.	<i>Eristalis intricarius</i> L.
<i>S. balteatus</i> Deg.	<i>Eriothrix rufomaculata</i> Deg.
<i>S. cinctellus</i> Ztt.	<i>Drymia hamata</i> Fln.
<i>Baccha elongata</i> F.	

Cnicus arvensis Robs. (5).

<i>Melanostoma mellinum</i> L.	<i>Eriothrix rufomaculata</i> Deg
<i>Sphaerophoria menthastris</i> L.	<i>Sarcophaga agricola</i> Mg.
<i>Eristalis arbustorum</i> L.	

Lapsana communis L. (2).

<i>Melanostoma mellinum</i> L.	<i>Syritta pipiens</i> L.
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Hypochaeris radicata L. (1).

Melanostoma mellinum L.

Leontodon autumnale L. (26).*Chilosia proxima* Ztt.*Ch. vernalis* Fln.*Platychirus manicatus* Mg.*P. peltatus* Mg.*P. sulcatus* Mg.*P. albimanus* F.*Melanostoma mellinum* L.*Catabomba pyrastris* L.*C. selenitica* Mg.*Syrphus albostriatus* Fln.*S. tricinctus* Fln.*S. lineola* Ztt.*S. ribesii* L.*Syrphus vitripennis* Mg.*S. corollae* F.*S. luniger* Mg.*S. balteatus* Deg.*S. cinctellus* Ztt.*Sphaerophoria scripta* L.*S. nitidicollis* Ztt.*Ascia podagraria* F.*Eristalis arbustorum* L.*E. pertinax* Scop.*Helophilus pendulus* L.*Syritta pipiens* L.*Drymia hamata* Fln.*Taraxacum officinale* Weber. (9).*Pipiza luteitarsis* Ztt.*Chilosia chrysocoma* Mg.*Platychirus manicatus* Mg.*P. albimanus* F.*Melanostoma mellinum* L.*Syrphus albostriatus* Fln.*S. vitripennis* Mg.*S. luniger* Mg.*S. balteatus* Deg.*Crepis capillaris* Wallr. (*C. virens* L.). (1).

Melanostoma mellinum L.

Hieracium boreale Fr. (12).*Platychirus manicatus* Mg.*P. albimanus* F.*Catabomba pyrastris* L.*Syrphus ribesii* L.*S. vitripennis* Mg.*S. luniger* Mg.*Syrphus balteatus* Deg.*S. cinctellus* Ztt.*Sphaerophoria scripta* L.*Eristalis arbustorum* L.*E. pertinax* Scop.*Syritta pipiens* L.*Euphrasia borealis* Towns. (7).*Platychirus albimanus* F.*Melanostoma mellinum* L.*M. scalare* F.*Syrphus cinctellus* Ztt.*Graphomyia maculata* Scop.*Phaonia pallida* F.*Lauxania aenea* Fln.*Veronica Beccabunga* L. (1).

Syritta pipiens L.

Veronica Chamaedrys L. (3).*Platychirus manicatus* Mg.*Ascia podagraria* F.*Atherigona varia* Mg.*Mentha arvensis* L. (2).*Platychirus albimanus* F.*Eristalis nemorum* L.

Stachys sylvatica L. (3).

Platychirus albimanus F. Rhingia sp.
Baccha elongata F.

E. Flowers without nectar.

Rosa canina L. (1).

Volucella pellucens L.

Rosa arvensis Huds. (2).

Eristalis intricarius L. Eristalis arbustorum L.

Phleum pratense L. (2).

Melanostoma mellinum L. Hylemyia variata Fln.

Dactylis glomerata L. (1).

Melanostoma mellinum L.

In studying the foregoing lists it will be noticed how very greatly the Cyclorrhapha preponderate. Indeed, of the Orthorrhapha only four species belonging to the Bibionidae (*Bibio johannis* L.) and the Empidae (*Rhamphomyia flora* Fln., *Empis trigramma* Mg., *Ocydromia glabricula* Fln.) have been seen, while of the Cyclorrhapha we have recorded 121 species distributed through the various families as follows: Conopidae (1 sp.), Syrphidae (76 spp.), Tachinidae (9 spp.), Muscidae (10 spp.), Anthomyidae (19 spp.), Cordyluridae (1 sp.), Sarcophagidae (3 spp.), Opomyzidae (1 sp.) and Sepsidae (1 sp.). It is thus evident that the Syrphid visitors greatly outnumber in species all the other Diptera put together, while of the 44 non-Syrphids only 14 were found on flowers in which the nectar was not freely exposed.

In a valuable and interesting paper Richards¹ gives a list of insect visitors to the flowers of *Rubus fruticosus* (agg.). A surprising feature of this list is the very small number of Diptera—eight only—recorded by him. We have observed 42, not merely as occasional visitors, but as regular and abundant frequenters of these flowers. Indeed, the most attractive to Diptera of all the flowers investigated were *Heracleum Sphondylium* (80) and *Rubus* (42). This preference is shown not only by the number of species but also by the numbers of individuals visiting the flowers.

¹ O. W. Richards, Studies in the Ecology of English Heaths; III. Animal constituents of the felling and burn successions of Oxshott Heath, *Journ. of Ecology*, 14, No. 2, pp. 245-281.

The comparatively small number of species taken on *Angelica sylvestris* (9) and on *Chaerophyllum temulum* (8) with epigynous thalamic nectaries like those of *Heracleum* was rather surprising. The umbels of *Chaerophyllum* are less showy, but those of *Angelica* are large and conspicuous.

The same sort of difference is found when *Potentilla reptans* with its two species of visitors is compared with *Rubus*. The flowers have similar perigynous thalamic nectaries. The larger amount of pollen in *Rubus* might have been invoked as a possible explanation were it not that the pollen output, flower for flower, in *Potentilla* is greater than in the very attractive *Heracleum*. Undoubtedly the attractiveness of the nectar- and pollen-producing part as a whole,—the inflorescence in *Heracleum* and *Rubus* and the individual flower in *Potentilla reptans*—may have something to do with the difference in the number of insect visitors, but the discrepancy between *Heracleum* and *Angelica* in this respect, both of which have the same kind of large and showy inflorescence and a similar structure of individual flower and nectary, forbids us to regard this as at all a complete explanation. *Sambucus nigra*, too, in spite of its large and showy inflorescence was not found to be a favourite with the Diptera nor was *Cornus sanguinea*.

The *Ranunculi* with the nectary covered by a scale showed a great preponderance—20 to 4—of the longer tongued Syrphids over the shorter tongued muscid type. Attention was called in our previous paper¹ to the attractiveness of *Convolvulus arvensis* for Syrphids. The shorter tongued Diptera are not nearly so much attracted. Of the 14 species found in this flower 11 were Syrphids.

Nearly all of the flies visiting the flowers with nectaries concealed in the corolla tube were Syrphids. The only others were *Eriothrix rufomaculata* Deg., *Drymia hamata* Fln., *Sarcophaga agricola* Mg., *Graphomyia maculata* Scop., *Phaonia pallida* F., *Lauxania aenea* Fln. and *Atherigona varia* Mg. In this group of flowers the Compositae appear to be the most frequently visited and of these *Leontodon autumnale* with its 26 species leads the way. Willis and Burkhill² called attention to the number of "short-tongued insects" (i.e. Diptera as a whole) that visited the flowers of this plant. They expressed the view that, "though so numerous, these insects are of little importance in fertilization." If the authors here wrote

¹ *New Phytologist*, 16.

² Willis and Burkhill, Flowers and Insects in Great Britain, *Ann. Bot.* 9, 1895.

"fertilization" as a synonym for "pollination" we are not able to agree with their statement. We have satisfied ourselves that the Diptera do play a very large part in the pollination of the flowers of this plant and other Composites. Indeed many of the short-tubed Compositae may be regarded as having pre-eminently Dipteran flowers. The nectar wells up in the tube and is easily reached by the Syrphids, Muscids, Anthomyids and Tachinids. Insects of these families are by far the most abundant visitors to the Asters of the Michaelmas Daisy section.

The markedly inferior attractiveness for Diptera of *Hypochaeris radicata*, *Lapsana* and *Crepis capillaris* is striking and not readily explicable.

Veronica is generally regarded as having peculiarly a Dipteran flower. We have convinced ourselves that these flowers are really pollinated in the manner generally described, but the attractiveness of *V. Beccabunga* and *V. Chamaedrys* for individuals and for species of Diptera is comparatively small.

Euphrasia, sometimes regarded as having "fly-flowers," did not prove to be particularly attractive. Our observations were limited to *E. borealis* which grows in great profusion on the Millstone Grit in North Derbyshire. A comparison of the visitors of this species with those of the longer-tubed *E. Kernerii* Wettst., *E. campestris* Jord. and *E. Rostkoviana* Hayne might prove interesting, but we do not think that any great difference would be found, as flowers showing greater diversity of tube length are frequented by much the same Dipteran fauna.

The nectarless flowers to which we have paid attention, namely *Rosa canina*, *R. arvensis*, *Phleum pratense* and *Dactylis glomerata*, have not yielded many species of Dipteran visitors—only 5 species in all. This seems to indicate that nectar rather than pollen is the usual object of the visits, though the Syrphids, Muscids, Anthomyids, Tachinids and Stratiomyids are undoubtedly pollen eaters as well as nectar suckers, as was pointed out by Hermann Müller long ago (*Fertilization*). The absence of *Stratiomyidae* from our records is noteworthy in view of H. Müller's observations.

The attractiveness of *Phleum pratense* for flies was unexpected. We have seen the plant with its inflorescences literally covered with *Melanostoma mellinum* and *Hylemyia variata*. They were quite distinctly engaged in eating pollen and were not merely making use of a temporary resting place. As stigmas and stamens were fully developed in different parts of the same inflorescence there can be no doubt that the flies were aiding in pollination. The visits to

Dactylis glomerata were also quite clearly purposive but this plant seems to be less attractive than *Phleum pratense*.

The longest-tongued genus of British Syrphids is *Rhingia*. Willis and Burkhill¹ state that what they term *Rhingia rostrata* occurred abundantly on *Centaurea* and *Stachys* but was never seen on any other flower. At the time when they wrote (1895) *Rh. rostrata* L. and *Rh. campestris* Mg. were not distinguished in this country and both species were referred to generally as *Rh. rostrata*. As a matter of fact *Rh. campestris* is the commoner species as was pointed out by Verrall² in 1901, who records *Rh. rostrata* from Barmouth only. We have taken it on *Centaurea nigra* at Barlow in Derbyshire, while *Rh. campestris* has been taken on *Rubus* and *Heracleum* as well as on *Centaurea* and *Stachys*.

According to Knuth³ the Conopidae, which appear to be purely suctorial, i.e. not pollen eaters, confine their attention almost exclusively to flowers with completely concealed nectar and of such they prefer social forms. We have only once taken a member of the Conopidae—*Conops flavipes* L.—as a flower visitor and this was on *Heracleum Sphondylium* which is social, but has the nectar very freely exposed.

It should be mentioned that most of our observations have been made in North Derbyshire near the edge of the moors. We hope to extend our attention to other flowers and to the Hymenoptera.

At the present time the Diptera are undergoing rapid revision and we fear that our nomenclature is in many instances archaic. That it has been brought up-to-date in some groups is due to our friend Dr W. J. Fordham, of Gateshead, and to him we record our grateful thanks.

¹ Willis and Burkhill, Flowers and Insects in Great Britain, *Ann. Bot.* 9, 1895.

² Verrall, *Syrphidae of Great Britain*, London, 1901.

³ Knuth, *Handbook of Flower Pollination*, English trans. Oxford.

REVIEW

THE CRETACEOUS FLORA OF WESTERN GREENLAND

The publication of Professor Seward's important work on the Cretaceous flora of Greenland¹ is a new illustration of the welcome fact that English palaeobotany is now taking up on a large scale the study of the fossil floras of the polar regions. In the past, the work on these floras has largely centred round the polar explorations carried out by the Scandinavian nations. By far the greater part of the material which formed the basis of Oswald Heer's extensive, if not always very critical, descriptive work had been collected by Swedish Arctic expeditions or during the Danish exploration of Greenland. Heer's work was continued by A. G. Nathorst, who introduced modern critical methods into the study of these plant-remains. As a result of his long field-work, Nathorst was able to demonstrate most convincingly before the International Geological Congress in 1910 that the remains of the Arctic fossil floras as a rule are preserved *in situ* and have not drifted from more southern latitudes: thereby a secure foundation was laid for all future phyto-geographical discussion of these floras.

In view of this historical development it is of particular interest to Swedish palaeobotanists to note that during the last two decades Cambridge has become, through the work of Professor Seward and his disciples, a new centre of activity in this field. The first important publication was Professor Seward's study of the remains of *Glossopteris* and other plants discovered by Captain Scott's expedition, through which the domain of the interesting Gondwana flora was extended to near the South Pole. Since Professor Seward's expedition to Western Greenland in 1921 that country has claimed the chief interest. The Cretaceous floras of the west coast have been dealt with not only in the memoir which forms the subject of these lines but also in a previous paper published in 1925 in the *Livre Jubilaire* of the Société Géologique de Belgique. Mr T. M. Harris has recently published an important account of the Rhaetic flora of the east coast prepared at the Botany School of Cambridge, and is at present engaged in collecting more material in the field in collaboration with the Danes. This recent activity, however, also connects with British polar exploration in the past: as Professor Seward reminds us, some of the very first fossil plants from Greenland described by Heer as early as 1866 had been brought home by British expeditions under Sir E. A. Inglefield and Sir Leopold M'Clintock about the middle of the last century.

The greater part of Professor Seward's memoir is occupied by a detailed description of material which he and Mr Holttum collected in 1921. The determination of the specimens of this flora is particularly difficult because Heer's diagnoses and descriptions are often rather summary and his illustrations, reproduced in lithographic print after mere contour drawings, are necessarily somewhat diagrammatic and not seldom inaccurate. For a satisfactory identification, indeed, it is often necessary to examine the type-specimens themselves, and the value of Professor Seward's revision of the flora is greatly increased by the fact that he has subjected these type-specimens to repeated examination during visits to Copenhagen and Stockholm. The comparison has in many cases led the author to unite species which Heer had described under separate names, and it is no injustice to the memory of the great pioneer in the field of Arctic palaeobotany to admit that these changes are as a rule undoubtedly justified. In regard to the important question whether, in critical cases, a wide or a narrow delimitation of species is to be preferred there is a feud of long standing between Professor Seward and the writer of these lines, who is necessarily not quite unbiased. I continue to believe that it is better to postpone identification, especially between forms belonging to floras which differ in time or space, than to risk premature identifications. Holding this

¹ A. C. Seward, "The Cretaceous plant-bearing rocks of Western Greenland." *Phil. Trans. Roy. Soc. London*, Series B, vol. 215, 1926.

opinion, I am inclined to believe that the author may occasionally have carried the process of identification too far. On the other hand, he has shown that in many instances Heer's identification of Greenland forms, chiefly, with European species, cannot be upheld. Through Professor Seward's work the relations between the Cretaceous flora of Greenland and those of Europe and other regions have therefore been placed on a much safer basis than before.

The determinations are in many cases confirmed by studies of cuticular structures, sporangia and other features of greater systematic importance. This application of modern methods marks a very great advance on all other comprehensive studies of these floras and has proved of great value in the welcome revision of Heer's work, which the author has so successfully brought to a close. An exhaustive criticism of the individual determinations cannot be attempted here: in the following only a few suggestions are put forward which have occurred to a reader who has no close personal knowledge of the material.

Among the rather few ferns the greatest interest is claimed by the genus *Gleichenites*, which is more abundant in the Cretaceous of Western Greenland than in any other fossil flora: one might, indeed, speak, as the author does, of veritable *Gleichenieta* as dominant plant-associations of Greenland in Cretaceous times. The author's use of the term *Gleichenites* has been criticised by Dr Berry; and it may be that objections can be raised against an emendation of Goeppert's genus on strict grounds of priority. But I entirely agree with Professor Seward in thinking that *Gleichenites* is to be preferred to the name of the recent genus. In this case there is not only the lack of sufficient proof of generic identity, in itself a strong argument for the use of a provisional designation, but, as pointed out by the author, some of the Mesozoic forms actually differ from recent *Gleicheniae* in having a greater number of sporangia in the sorus, sometimes as many as 12-30. On the other hand, the author has been able to put forward additional evidence of relationship between the Greenland plants and the recent genus in the anatomical structure of the rachides referred to the new species *G. Porsildi*.

The definition of *Gleichenites Gieseckiana* is a good instance of the radical revision of Heer's determinations: in this species are placed specimens referred by Heer to no less than ten other species! *Gleichenites Porsildi* is a new name given to a form of which the first described specimens were referred by Heer to his *Gleichenia rigida*. The type of that species has been shown by the author to be a form of *Lacopteris*, which should naturally retain the specific name; and a new name had to be given to the form represented by the other specimens. To *G. Porsildi* are referred specimens described by Heer under six other species but differing for the most part from the type-specimens of those species. Two of these species, however, *Aspidium Schouwii* Heer and *Cyathea angusta* Heer, are identified in their entirety with *G. Porsildi*, and it may be questioned why one of these older names has not been used.

The impressions referred by the author to *Lacopteris rigida* (Heer) Sew. no doubt belong to that genus; but this does not necessarily prove that the same is the case with the species referred by Nathorst and the writer of these lines to *Nathorstia* Heer. In the Patagonian specimens placed in that genus I am unable to detect the annulus-like structure which the author claims as confirming his opinion that the species belongs to *Lacopteris*. It is to be hoped that new material will be found with the sori sufficiently well preserved to show unequivocally whether the sporangia are free or not. The sori of *Lacopteris* shown in Pl. 8, Figs. 59 and 60, and in Text-fig. 8 c, are curiously like those of *Gleichenia* in the small number of sporangia and in the marginal position of the annulus. It is of great interest that the author has been able to identify the characteristic Wealden species *Sphenopteris (Onychiopsis) psilotoides* not only in his own material but also in specimens referred by Heer to various other species. *Sphenopteris dentata* (Velenovsky) is a species first described from Bohemia under the generic name *Kirchnera*. The author records this species from Greenland; but the figures quoted from Velenovsky's work have reference to the other species, *Kirchnera arctica* Vel., and it is probably this species that is meant; both species, however, may be identical. With the same species the author compares Heer's *Asplenium Nauckhoffianum*, but the type-specimens of that species, as I have mentioned elsewhere, have peculiarly truncate lobes different from those of Velenovsky's species.

The Cycadophyta are few, as always in the Greenland Cretaceous, only five species being discussed. In *Ptilophyllum arcticum* is included, no doubt with justification, the species described by Heer as *Zamites brevipennis*. It is rather doubtful to which genus this and other species placed by Heer in *Zamites* should be referred. It is true that they differ from the typical species of *Zamites*, but, on the other hand, *Ptilophyllum*, in my opinion, should be reserved, in accordance with Feistmantel's definition, for fronds with decurrent pinnae.

Among the Ginkgoales the most important species is the one named *Ginkgoites pluripartita*. The author gives a convincing illustration of the variation in leaf-form which has led him to include in this species—originally described from the Wealden of Germany—two species referred by Heer to *Ginkgo* and *Baiera*, respectively. Under the name of *Phoenicopsis Steenstrupi* n. sp. is described a small leaf, the cuticular structure of which is splendidly illustrated; it might have been profitable to discuss also the possible relation of this leaf to the very similar genus *Feildenia*.

In the study of the Cretaceous Coniferales of Greenland Professor Seward's work marks an important forward step, not least through the attention paid, whenever possible, to the cuticular structures. One of the species showing the structure of the epidermis is described as *Pityophyllum crassum* n. sp.; it may be suggested that this form ought to have been compared with the well-known Wealden species *Abietites Linckii*, which, as I have been informed by Dr R. Florin, has a very similar cuticle.

The Monocotyledons, as always in fossil floras, are few and to some extent doubtful. The genus *Macchintockia*, which is held by the author to be most nearly allied to *Smilax*, is represented by a somewhat fragmentary specimen. Another specimen figured under the name of *Flabellaria* (?) sp., is still more fragmentary but of great interest because it may possibly, as the author doubtfully suggests, be the remains of a palm and thus represent a group of plants not hitherto known from the Greenland Cretaceous.

The Dicotyledons are always the crux in the determination of fossil plants; and the writer of these lines declares himself incompetent to express any definite opinion regarding the correctness of the determinations. The nomenclature of fossil dicotyledonous leaves illustrates the prevailing uncertainty: the recent genera and provisional names formed by the addition of *-phyllum* are used variously by different authors. Professor Seward generally adopts names of the second type—in my opinion wisely—but in one or two cases the recent generic names are used on what I believe to be rather slight evidence. Thus the name *Quercus* is given—though, as the author states, with some hesitation—to a small fragment identified with *Quercus Johnstrupi* Heer. Ettingshausen and Krasan are quoted as authorities for the statement that this species agrees closely with the recent *Quercus sessiliflora*; but I am unable to find any specific resemblance between the recent leaves and the single small fragment shown in Text-fig. 22. The discussion of the genera *Platanus* and *Platanophyllum*, both of which names are used, suggests the need of a general revision of all forms referred by various authors to these genera and to *Araliaephyllum*; for this purpose, however, a monographic treatment of all corresponding recent species—quite outside the scope of Professor Seward's work—would be necessary. It may be questioned whether the specimen in Text-fig. 30 and the one with straighter veins shown in Pl. II, Fig. 116, both identified with *Platanus Newberryana*, really belong to the same species.

The description of the species is followed by a very interesting general discussion dealing with the relationship of the flora to those of other regions, with the climatic conditions, and the appearance of the Angiosperms. The whole Cretaceous flora of Western Greenland is in these considerations treated as a whole. In the present state of our knowledge of the stratigraphy this is probably the only possible course; but it is greatly to be hoped that in the future it will be possible to discuss the different horizons separately. The phytogeographical relations of this flora are of quite unusual importance, because they are intimately connected with the great problem of the first appearance of the Angiosperms, which undoubtedly has also an important geological aspect. The author gives an admirable exposition of this side of the question. A consideration of the table of distribution (Table B, p. 147) clearly demonstrates that the flora is a mixture of two components, with different geo-

graphical relations, and that of these components one is formed by the Angiosperms, the other by the older element of Pteridophyta and Gymnosperms. Taking the flora as a whole the greatest resemblance is to the Cretaceous floras of Dakota, New Jersey, Sakhalin and Bohemia. If the Angiosperms are excluded, an agreement that is just as great or even greater is found with the Upper Jurassic and Wealden floras of Great Britain, the European Continent and Spitsbergen. In the Greenland Cretaceous a number of Angiosperms are thus found together with elements characteristic of the Upper Jurassic and the Wealden, whereas in Europe and other regions these elements occur without any admixture of Angiosperms, that group appearing first at a later epoch. The author concludes that the Cretaceous flora of Greenland is composed of an older element of Jurassic and Wealden types, which immigrated from the south, and a younger flora of Angiosperms, which originated in the Arctic and then spread southward. This is a most interesting point of view, which will probably prove fruitful in the discussion of these problems. At present the evidence of a northward migration of Upper Jurassic and Wealden plants is perhaps not quite conclusive. We have no knowledge of the vegetation which these immigrants replaced, and it is not quite excluded that before the beginning of the Cretaceous period Greenland already had a vegetation of the same kind as that of Europe. The Jurassic-Wealden plants of both these regions may have been evolved within their later range of distribution from the preceding Rhaetic-Middle Jurassic vegetation, which seems to have been very evenly distributed from low latitudes to far north of the Polar Circle. It is true that in regard to the Pteridophytes and the Gymnosperms the Greenland Cretaceous shows a closer agreement with the Upper Jurassic and Wealden of Europe than with the Mesozoic of Spitsbergen. But the difference, as shown by Professor Seward's table of distribution, is not great and may be due to the fact that the floras of Spitsbergen are probably on the whole somewhat older and certainly less known.

The concluding part gives an interesting exposition of the bearings which the Cretaceous vegetation of Greenland has on the question of climatic changes. The author's remarks on this subject can be summarised as a sound reaction against overestimation of the geographical changes implied by a comparison between the Mesozoic and the recent floras. He expresses the opinion that "the change needed to enable a sub-tropical flora to exist in high latitudes is not great," and gives an estimate of the rise in temperature necessitated to make middle Norway habitable for a flora such as that now flourishing in the North Island of New Zealand. One can but agree with the author that the climatic changes demanded "can be accounted for without calling to our aid explanations based on purely hypothetical departures from the order of nature." It is perhaps more doubtful whether, as Professor Seward suggests, the phyto-geographical differences between the past and the present can be explained, to any considerable extent, by assuming that genera now confined to the Tropics were represented in Cretaceous time by more hardy species. If the gradually decreasing temperature in high latitudes since the Cretaceous time has had any influence on the hardiness of newly evolved species—which touches the vexed general question of environment as affecting the formation of new species—the result would rather be expected to have been the opposite. Granting this influence, any stock that has passed through the vicissitudes of a gradually deteriorating climate would rather be expected to have evolved hardier forms. At any rate, the species more sensitive to low temperatures ought to have been the first to succumb. The novel factor in competition introduced by the appearance of a new type of vegetation, deciduous angiospermous trees and shrubs, may also have been of some importance. It is of great interest in this connection that the author hints at the favourable conditions which the strong annual periodicity prevailing in the arctic regions, not only in regard to temperature but also to insolation, may have offered to the development of deciduous angiospermous trees.

The memoir is liberally illustrated, mainly by photographs and also by drawings and microphotographs showing anatomical details. The reproduction is very good and shows that autotype can in many cases be used with advantage for palaeobotanical illustrations—which generally require the best possible rendering in print—instead of the more expensive collotype.

The writer of these lines has learned with much pleasure that Professor Seward does not intend to conclude his studies of the Cretaceous floras of Greenland with the publication of the present memoir, which is warmly welcomed by other workers. It is to be expected that the study of extensive material now sent to Cambridge from the museums of Copenhagen and Stockholm will result in other important works on the Cretaceous flora of Greenland. I wish to conclude these lines by expressing the hope that facilities will be found for publishing the future contributions to the full extent, in regard to both text and illustrations, demanded by the difficulty and the high importance of the subject.

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CHAPTER III

SYMPETALAE AND MONOCOTYLEDONS

SYMPETALAE (3550 gen., 50,500 sp.)

THE Sympetalae, as a whole, are undoubtedly more advanced than the Archichlamydeae, but if, as is now generally the accepted belief among botanists, the former are polyphyletic in origin, it may very well be that certain groups developed much sooner than others. Further, as a result of the continued process of differentiation in all the orders of the dicotyledons, certain families among the Archichlamydeae may be more recent and more advanced than some families among the Sympetalae. The Sympetalae are not without representation as far back as the Cretaceous, and several families of the Archichlamydeae have almost certainly been evolved since then. Yet, in a general way, the Sympetalae show their high development in being predominantly herbaceous and, on the whole, extensively adapted to modern conditions, either outside the tropics or within the tropics in the drier regions or in open grassland habitats. In the moist tropical forest habitats, they are relatively less abundant. Tree forms are comparatively rare among them. In so far as they are represented in tropical forest, they show the effects of the biota, and consist largely of climbing forms or herbaceous undergrowth.

Nevertheless, within each circle of affinity, they continue to illustrate extremely well the general principles set forth in chapter II. Since the relationships of the families are better understood, on the whole the story of their evolution is clearer than it is among the Archichlamydeae.

ERICALES. This relatively primitive order includes the Ericaceae (77 gen., 1550 sp.), the Epacridaceae (23 gen., 340 sp.), the Pirolaceae (10 gen., 30 sp.), the Diapensiaceae (6 gen., 9 sp.) and the Clethraceae

(*Clethra* 30 sp.) with the degenerate family of root parasites, the Lennoaceae (3 gen., 5 sp.). The great central and most widely distributed family is the Ericaceae, of which, species of *Andromeda* are said to go back to the Cretaceous. They may possibly be connected with the Geraniales or Rutales. The shrubby Rutaceae, with their occasional sympetaly (as in the tribe Cusparieae), afford us a hint of a possible starting-point for the Ericaceae. As we have seen, the shrubby Rutaceae are, at the present time, mostly mountainous or warm temperate in distribution while the tree forms of the same family, which are floristically more primitive, are more tropical. The Ericaceae themselves are not all sympetalous. The small tribe Ledeeae with four genera in North and South America, and one in Japan, are polypetalous. The chief centre of the tribe Rhododendreae is the mountainous region of South-East Asia from South China to the Himalayas. The small tribe Phyllodoceae are mostly North American and circumpolar. All these belong to the subfamily Rhododendroideae, an ancient mountain and temperate type. The subfamily Arbutoideae may be even more ancient. The tribe Andromedae are mostly North American, but include one genus from the mountains of South-East Asia and one (*Agauria*), with seven species, on the mountains of tropical Africa; the tribe, Gaultherieae is very widely distributed, having *Gaultheria* in America, Japan, the Himalayas and Tasmania, and four other genera (India, Malaya, Tasmania, New Zealand, South-East Australia, North and Central America); the tribe Arbuteae include *Arbutus* (Mediterranean region, Western Asia and North America), *Arctostaphylos* (north temperate and arctic) and *Arctous*, circumpolar. The subfamily Vaccinioideae (which, according to Wernham may have had a distinct origin, possibly from the Rosales) include 20 genera, chiefly from the Himalayas, and various tropical mountains in South America. The genus *Vaccinium* itself is mainly north temperate, but occurs in the Andes and in the mountains of Madagascar. Finally the subfamily Ericoideae are particularly characteristic of the mountainous south-western region of the Cape where *Erica* alone has 480 species, and there are many smaller genera. The Ericoideae extend along the African mountain ranges to Europe; *Erica arborea* on the tropical African mountains and in the Mediterranean may represent a rather ancient type.

The distribution of the Ericaceae, as a whole, would indicate that they represent another ancient, temperate type, which probably originated on the mountain ranges of the world. Among the Archi-

chlamydeae, families like the Proteaceae, Grubbiaceae, Bruniaceae, Penaeaceae, Geraniaceae, the shrubby Rutaceae, Empetraceae and others have probably had a similar origin. The fact that the Epacridaceae, which differ from the Ericaceae chiefly in the isomery of the stamens, have almost entirely taken the places of the latter in Australia, is significant. It would seem to point to a separation of the two families since the connections of Australia and the other continents were broken. The Epacridaceae do, however, have a few representatives outside Australia (in India, New Zealand, Hawaii and South America). All the families of the Ericales, however ancient they may be, are to be considered derivative; and if they are to be connected, as is generally believed, with the Rutales, then their ancestors were again more tropical, but the detailed lines of origin are no longer very obvious. The tropical origin and differentiation of the Geranales and Rutales have already been dealt with.

PRIMULALES. In this order, the relatively tropical or subtropical Myrsinaceae (32 gen., 1000 sp.), a family of trees and shrubs, contrasts with the more advanced and more temperate Primulaceae (28 gen., 250 sp.), a family of herbs. Among the Myrsinaceae, the petals are free in *Embelia* which has about sixty species in the tropics of Asia and Africa. The more subtropical or more xerophytic genus, *Maesa*, on the other hand, shows advance in having the ovary inferior or half inferior. The small tropical family, Theophrastaceae (4 gen., 70 sp.), are allied to the Myrsinaceae. The Plumbaginaceae, (10 gen., 280 sp.), though allied to the Primulales, are not so closely connected. They show advance in the reduction of the ovules to one and are commonest in halophilous habitats.

The EBENALES are the third order of the Pentacyclidae (which also include the Ericales and Primulales). The Ebenales are almost entirely tropical or subtropical trees, including the Sapotaceae (50 gen., 650 sp.), Ebenaceae (5 gen., 320 sp.), Styracaceae (8 gen., 120 sp.) and Symplocaceae (*Symplocos* 300 sp.). The order is generally considered to have had two distinct lines of development, one represented by the Sapotaceae and the other by the remaining families. In the Sapotaceae, rather more advanced genera, e.g. *Mimusops* and *Sideroxylon*, extend outside the tropics particularly along seashore habitats.

Similarly in the Ebenaceae, genera like *Royena* and *Euclea* have many species adapted to drier subtropical conditions and are, on the whole, more advanced than the more tropical genera *Diospyros* and *Maba*.

The *CONTORTAE*. In this order the Oleaceae (25 gen., 420 sp.) are somewhat isolated. They show advance in having the ovules reduced to 2 or 1 per loculus, and the stamens reduced to two and are mostly drier subtropical or warm temperate in distribution. The Ash (*Fraxinus excelsior*) with its reduced polygamous flowers is a native of Britain. The other families, Loganiaceae (33 gen., 550 sp.), Apocynaceae (165 gen., 1300 sp.), Asclepiadaceae (267 gen., 2200 sp.) and Gentianaceae (71 gen., 900 sp.) come closer together, and all illustrate our general principles of ecological differentiation extremely well.

The Loganiaceae are floristically the most primitive, and are mostly tropical or subtropical with a few warm temperate representatives. The subfamily Loganioideae are more primitive and more tropical than the Buddleioideae. The Apocynaceae are more advanced and within the tropics show the effects of the biota in their prevalent climbing habit. Some are shrubs adapted to somewhat drier subtropical conditions, and one or two, e.g. *Vinca* spp., have penetrated into temperate regions. The higher Apocynaceae connect with the Asclepiadaceae, the Periplocoideae being a transitional tribe with loose pollen grains. The Asclepiadaceae under forest conditions are mostly climbers which become increasingly xerophytic in the drier types of subtropical savannah-forest and scrub. The climbing habit is retained by several distinct tribes, ecological evolution, as often happens, thus cutting across floristic evolution. Many very large genera of the family have adopted a geophytic habit under grassland conditions. Some species have penetrated into temperate regions. A few are common weeds. The most highly specialised of all, floristically and otherwise, are the desert or semi-desert forms, particularly the tribe Stapelieae so characteristic of the drier parts of South Africa.

The Gentianaceae have not developed in such a specialised direction in response to insect visits, but they are, nevertheless, more advanced than the others in having the ovary usually unicellular and in their prevalent herbaceous habit. A few are shrubs, but the great majority are herbs. They occur all over the world and have become differentiated to suit all kinds of habitats. They include forest and grassland herbs, temperate region plants, arctic and alpine plants, halophytes, saprophytes (*Voyria*), marsh plants and water plants (*Limnanthemum*).

TUBIFLORAE. The Polemoniaceae (13 gen., 280 sp.) are a rather isolated small family, chiefly North American, but represented also in South America, Europe and Asia. They usually have three

carpels, and it is difficult to say what their history or exact relationships have been.

The Convolvulaceae (45 gen., 1150 sp.) have the flowers usually large and not crowded into dense inflorescences, and probably represent the modern development of the stock (not very distinct from that of the Contortae) that gave rise to all the other families of the Tubiflorae. The tropical forms include a few small trees, many shrubs and climbers as well as herbs; in temperate regions herbaceous forms are commoner, including annuals. One widespread genus *Cuscuta* has become parasitic.

From the original stock, two other small families have probably evolved directly—the Hydrophyllaceae (17 gen., 180 sp.), a family of herbs and undershrubs, chiefly North American with a few in South America, Asia and Africa, and also the Nolanaceae (3 gen., 50 sp.) on the west coast of South America.

There remain two great diverging lines, leading to the Personales on the one hand and the Lamiales on the other, if we adopt Bentham and Hooker's names. The Solanaceae (83 gen., 2100 sp.) come somewhere near the ancestral forms of the Personales. They consist of trees, shrubs and herbs with their main centre of distribution in Central and South America, extending into the temperate regions. The tropical tribes, Cestreae and Salpiglossideae, with the embryos straight or only slightly curved are relatively primitive in some respects, but the Salpiglossideae once more illustrate the effects of the biota, and in the more superficial flower characters show advance in the reduction of the stamens to four or two. Zygomorphy in the flowers, as we have seen, may occasionally develop in tropical representatives to a greater extent than in temperate, but, as a rule it is confined to subordinate and derivative types of plant form. The Bignoniaceae (109 gen., 670 sp.) are also a rather primitive member of the Personales. They are a family of trees and shrubs, often climbing, tropical and subtropical in distribution, mostly in Brazil. One genus *Catalpa* is common to the Old and New Worlds. The Bignoniaceae show interesting responses to drier subtropical conditions e.g. in the South African genus *Rhigozum*. The small families Pedaliaceae (17 gen., 70 sp.) and Martyniaceae (3 gen., 10 sp.) of seashore or desert or ruderal plants are allied to the Bignoniaceae, but distinctly derivative and more advanced.

The Scrophulariaceae (210 gen., 3000 sp.) connect with the Solanaceae, through the tribe Verbasceae. Ecologically they show a large amount of interesting differentiation. There are a few tropical

or subtropical tree forms (e.g. *Paulownia*, *Halleria*), several shrubby genera adapted to drier subtropical conditions (e.g. *Bowkeria*), several climbers (e.g. *Maurandia*, *Rhodochiton*), an epiphytic genus (*Dermatobotrys*), marsh and aquatic forms (e.g. *Limosella*, *Diclis*), a large number of hemiparasitic genera (e.g. *Euphrasia*, *Bartsia*, *Pedicularis*, *Cycnium*, *Melasma*, *Striga*), a number of holo-parasites (e.g. *Harveya*, *Hyobanche*) and a great many subtropical and temperate herbs. In allied small families the process of differentiation is carried still further. There is reduction of the ovules in the Selaginaceae (often included as a tribe of the Scrophulariaceae). The Globulariaceae (3 gen., 20 sp.) have the ovary unilocular with one ovule. The Orobanchaceae (12 gen., 140 sp.) are parasites chiefly north temperate in distribution. The Lentibulariaceae (6 gen., 260 sp.) are marsh or water plants usually insectivorous. The Gesneraceae (97 gen., 1150 sp.) are a larger allied family which show a tendency to epigyny. They include some woody plants but are mostly herbaceous and are often rather common as undergrowth in tropical and subtropical forest.

The Acanthaceae (214 gen., 2400 sp.) are also particularly characteristic of the forest margins and forest undergrowth in tropical and subtropical regions representing a highly specialised response to the effects of the biota. It is again interesting to note that the more primitive subfamilies, Nelsonioideae, Mendonsioideae and Thunbergioideae, are distinctly more tropical than the Acanthoideae, many members of which are adapted to grassland conditions in subtropical regions, and some extend into temperate regions, e.g. in the Mediterranean countries, North America, Australia and South Africa.

The small family Myoporaceae (5 gen., 90 sp.) found chiefly in Australia and the neighbouring islands are placed by Engler near the Acanthaceae but Bentham and Hooker included them in the Lamiales.

The Boraginaceae (97 gen., 1500 sp.) come nearest to the ancestral stock of the Lamiales, as the Solanaceae do in the case of the Personales. The Boraginaceae illustrate very well the same lines of differentiation. The floristically primitive tribes, with their styles inserted at the apex of the ovary, and their fruits drupaceous, are all, more or less, tropical or subtropical and woody including the Cordioideae (3 gen. of which *Cordia* is the largest with 230 sp.), the Ehretioideae (10 genera) and the Heliotropoideae (3 gen. of which *Tournefortia* has 120 sp. and *Heliotropium* 220 sp.). The more advanced herbaceous Boraginoideae, on the other hand, with their gynobasic styles and schizocarpic fruits, are chiefly temperate. The

Mediterranean region is an important centre of their distribution. The Labiate (170 gen., 3400 sp.) show advance in their zygomorphy and efficient protection of fruit and seed by the persistent calyx, etc. Like the Acanthaceae, they are rather prominent as forest margin plants in subtropical regions, but they have become more widespread and differentiated in temperate regions. The majority are under shrubs and herbs often showing a certain degree of xerophytism, particularly in the prevalent production of ethereal oils. The Mediterranean region is again one of their most important centres. The Verbenaceae (80 gen., 900 sp.) represent a sideline development from the Lamial stock. Several have remained rather primitive with straight or half-inverted ovules, e.g. *Avicennia*, one of the tropical Mangroves. The warm temperate mountain representatives at the Cape show advance in having basal inverted ovules, but have retained endospermous seeds and in several genera have more or less regular flowers, i.e. they show advance in some respects but not in others. We have already noted many features of this mountain flora which indicate that it represents rather an ancient temperate type. As in the case of many other families (Penaeaceae, Grubbiaceae, Bruniaceae, Leguminosae, Thymelaeaceae, etc.), the Verbenaceae in mountainous regions such as South Africa have produced ericoid forms (e.g. *Stilbe*, *Euthystachys*, *Eurylobium*, etc.).

The Plantaginales (Plantaginaceae) have three genera, viz. *Bougueria* (1 sp. in Andes), *Litorella* (1 sp. in South America, and 1 in Europe) and *Plantago* (200 sp. cosmopolitan, but chiefly temperate). The affinities of the family are uncertain. They probably represent degraded forms allied to the Tubiflorae.

INFERAEE. The epigynous Sympetalae are considered to be the highest evolved group of flowering plants. Though the number of families included are few, the number of species is about 22,000 or not much less than one half of all the Sympetalae.

Engler (following Eichler) includes the Cucurbitaceae (97 gen., 750 sp.) among the Inferae, though they have also been placed near the Passifloraceae or near the Loasaceae and Begoniaceae among the Archichlamydeae. Whatever their exact affinities, there is no doubt that they are a rather highly evolved family, consisting of herbs, chiefly climbing and annual, found in the warmer regions of the world, and once more in their derivative character showing the influence of the biota. Engler divides the other Inferae into the Rubiales and Campanulatae, the latter including the Compositae, which are considered to be connected with the Campanulaceae. Bentham and

Hooker and other writers have connected the Compositae more closely with the Dipsaceae (included by Engler in the Rubiales).

RUBIALES. In this order the Rubiaceae (400 gen., 5000 sp.) are relatively primitive. Of the two subfamilies, the Cinchonoideae, with two or more ovules in each loculus, are more primitive and distinctly more tropical than the Coffeoideae which have only one ovule in each loculus. Both subfamilies are mainly woody and, at the same time, both have produced some herbaceous genera adapted to drier or colder conditions, e.g. *Oldenlandia* among the Cinchonoideae and *Galopina*, *Anthospermum*, *Spermacoce*, *Hydrophylax*, *Richardsonia* and the tribe Galieae among the Coffeoideae. The Galieae are a rather advanced tribe adapted to temperate conditions. The whole family again illustrates very well the general lines of ecological differentiation among the Angiosperms, the moist tropical forms primitive, the drier subtropical forms and the temperate forms all derivative and more advanced.

The Caprifoliaceae (11 gen., 350 sp.) are mainly north temperate with a few representatives on tropical mountains. They show advance in the marked tendency towards zygomorphy (e.g. in *Lonicera* with 100 sp. or more than one-fourth of the whole, as well as in others), in the oligomery of the androecium, as seen in *Dipelta* and *Linnaea*, and in a slight tendency towards aggregation of the flowers.

The Adoxaceae include only *Adoxa moschatellina* which is widespread over the north temperate zone. It shows advance in all its features, being a low herb, with compound leaves, and underground storage in a creeping rhizome. Its flowers are aggregated into globular heads with the terminal flowers usually tetramerous, the others pentamerous.

The Valerianaceae (10 gen., 350 sp.) are temperate or mountainous in their distribution, and consist of herbs with asymmetrical flowers aggregated in cymose panicles. The corolla is often spurred at the base, and the calyx often forms a pappus after flowering as in the Compositae. The stamens are from one to four, epipetalous, and there is only one ovule. Some are annuals, but the majority are perennials with underground rhizomes. All those features show advance. The Dipsaceae (10 gen., 160 sp.) are also temperate and mountainous in distribution, with the Mediterranean region as one of their main centres. They again show advance in being herbaceous, with the flowers aggregated, and showing zygomorphy and division of labour, and in having the ovules reduced to one. The calyx again plays a part in seed dispersal.

Not only then does the differentiation of the central and most primitive family of the Rubiales, the Rubiaceae, illustrate our general principles extremely well, but the differentiation of the order Rubiales, as a whole, shows how the same principles apply on a larger scale, and within a wider circle of affinity. The relatively advanced characters of all the temperate families are very striking.

CAMPANULATAE. The vast majority of the plants belonging to this order are herbaceous and they are all, more or less, of an advanced type floristically. The Campanulaceae (65 gen., 1500 sp.) are the most heterogeneous of the families having the ovary not always quite inferior, and the petals not always quite united. The ovary is usually multilocular and multiovulate, but there is a marked tendency towards a bicarpellary condition which rarely becomes unilocular (e.g. in *Merciera*). The anthers may be free, but they tend towards union in the Lobelioideae, where the corolla is zygomorphic. There is a tendency also towards aggregation of the flowers in some, e.g. *Jasione* and *Phyteuma*. In a word, the Campanulaceae show the beginnings of various lines of advance, which have reached their culmination in the Compositae, and were also seen, to some extent, in the Valerianaceae and Dipsaceae. As in the case of these families the distribution of the Campanulaceae is in the main temperate or mountainous. The tree Lobelias of the African mountains reach a height of 15 ft. and are a very interesting type of plant form. There are a few, small herbaceous families among the Campanulatae: the Goodeniaceae (11 gen., 300 sp.) chiefly Australian, the Brunoniaceae (*Brunonia*) Australia and Tasmania, the Stylidiaceae (6 gen., 120 sp.) Australia, South America and Asia, and the Calyceraceae (4 gen., 25 sp.) South America, each of which illustrates certain rather specialised and minor lines of development, which it is unnecessary for our present purpose to describe in detail.

The Compositae (950 gen., 13,500 sp.). All authorities are agreed that the Compositae are the most highly evolved and successful of all plants, and best adapted to modern environmental conditions. While they are quite cosmopolitan in their distribution, they are relatively rather scarce in the moist tropical regions and except for a few climbing species are hardly represented in tropical rain forest. They are, on the other hand, abundant in the drier subtropical and temperate regions. They are very common on tropical mountain ranges where woody types are characteristic, including tree Senecios and many shrubby forms, cushion forms, etc. There are a few tree forms adapted to drier subtropical or psammophilous habitats, e.g.

Tarchonanthus, *Brachylaena*. But the vast majority are undershrubs or herbs. In grassland areas with increasing aridity it is a very significant fact that Composite dwarf shrubs often become completely dominant as in the transitional areas between grassland and Karroo in South Africa. Many annual and succulent Composites are interspersed, and these and other types of extreme xerophytes belonging to the family become increasingly characteristic of semi-desert and desert regions. Herbaceous Composites are abundant all over the temperate regions. Annual forms are common as weeds in cultivated land and waste places as well as in desert regions. The annual type of Composite may be looked upon, in a general way, as the most highly evolved of all plants.

The geographical distribution of this great family lends the strongest possible support to the view that the moist tropical forest flora is relatively primitive. The Compositae are not represented there except for one or two subordinate forms. On the other hand, they have everywhere taken possession of the types of habitat which may be regarded as relatively modern. It is interesting to note in passing that Small (1920), who has dealt with the inter-relationships of the tribes, and the evolutionary history of the family as a whole in great detail, regards the family as having had a mountain origin. As we have seen, a great many, perhaps the majority of temperate families, have probably originated on the mountain ranges of the world, often apparently in the southern hemisphere, where the mountain ranges, in Africa at least, being of Permian age or older, have a much longer geological history than in any other part of the world. The various mountain ranges, however, which began to be built up at the close of the Cretaceous, are quite old enough to have seen the origin of much of the modern temperate flora, including the Compositae.

MONOCOTYLEDONS (1950 gen., 26,000 sp.)

The general question of the origin of the Monocotyledons and their relationship to the Dicotyledons need not be discussed here at any great length. Many distinguished authorities have preferred to consider that the Monocotyledons and Dicotyledons represent two distinct lines of evolution, e.g. Kny, Drude, Engler, Warming, Coulter and Chamberlain and others. Many other writers are strongly inclined to adopt the view that the Monocotyledons have been derived from the Dicotyledons. Miss Sargent (1902, 1904) has laid stress on the general tendency towards a geophilous habit among the

Monocotyledons, and derives them from dicotyledonous ancestors by means of syncotyly, i.e. the fusion of two cotyledons to form one. Union of the cotyledons to a greater or less extent is seen in many of the Ranunculaceae as well as in other dicotyledons (e.g. *Oxalis*, *Podophyllum*, *Rhizophora*, *Polygonum*). Since such cotyledonary fusion among dicotyledons is accompanied in practically all cases by shortened and thickened hypocotyls, and by the formation of underground storage organs of some kind or other, Miss Sargent has inferred that the general condition of monocotyledony is associated with a geophilous habit and that, therefore, the Monocotyledons, as a group, have evolved through adaptation as geophytes. The Liliaceae, according to this theory, form the central group among the Monocotyledons.

Considered in relation to our own viewpoint it may be pointed out that underground storage, as indeed storage of all kinds, is usually a response to a resting season. Geophytes are not prominent under uniformly moist tropical forest conditions. Even members of typically geophytic families have little underground storage if they belong to forest habitats in the tropics, e.g. *Clivia*, *Kniphofia*, etc. Geophytes only become abundant and highly differentiated in subtropical areas with a pronounced resting season. At the same time, a certain amount of storage does take place in subordinate forest species among epiphytes, climbers and forest margin herbs. So our general theory does not require us to argue that Miss Sargent's ideas are necessarily incorrect.

Those who prefer an origin for the Monocotyledons by means of "heterocotyly" (i.e. by the ultimate suppression of one of the cotyledons) connect them through the Araceae, with such typically tropical forest margin herbs as the Piperales (*Peperomia*). This view has been adopted by Hill, Lotsy, Henslow and others. For a fuller discussion of the literature of the subject, Bancroft (1914) should be consulted. Henslow (1893, 1911) looked upon the whole of the Monocotyledons as derived from Dicotyledons through "self-adaptation to a moist or aquatic habit." Most authors are inclined to look upon such tree-forms as do occur among the Monocotyledons as derivative, though there are some, e.g. Lindinger (1910), who regard them as primitive. All these general theories do not really carry us very far.

Whether the Monocotyledons were derived from the Dicotyledons or not, it is entirely in accord with our general theory to suppose that the earliest Monocotyledons were either marsh or forest margin

types and, as a matter of fact, this is also in agreement with any of the numerous theories that have been put forward regarding their origin. I have suggested elsewhere (Bews, 1925, p. 46) that if we are prepared to assume that the early Monocotyledons were marsh forms, and they behaved like modern plants of the same type, then they would tend to become widely distributed rather quickly. Marsh plants and aquatics probably throughout their history have remained to some extent independent of climatic differentiation. It is well known that marsh species tend to be widespread through different climatic areas at the present time. It is not surprising, therefore, to find that among typically aquatic or marsh groups such as the Helobiaeae, distribution does not throw much light on phylogeny or on their general differentiation. Nevertheless, a careful analysis of the distribution and phylogeny of the different orders of the Monocotyledons does tend to show that as among the Dicotyledons, the influence of the biota under moist tropical conditions has resulted in the production of specialised subordinate types of plant form, and likewise the response to drier and colder conditions has in general meant evolutionary advance.

It is interesting also to note that in their primitive marshy habitats their peculiar habit of growth with underground rhizomes and tufted aerial shoots has enabled many of the Monocotyledons to assume complete dominance while in drier situations the great family of the grasses have succeeded in completely conquering and dominating enormous areas of grassland, a type of vegetation different in many essential features from anything that could have preceded it. This has had a profound effect on the evolutionary history, not only of other derivative types of plant form, but also on the animal kingdom. The grasses, directly or indirectly, are the chief food of nearly all the mammals.

In summarising the distribution, phylogeny and ecological differentiation of the orders and families of Monocotyledons, Engler's system of classification is again followed.

PANDANALES. The screw pines or Pandanaceae (3 gen., 240 sp.) are trees and shrubs of the tropical regions of the Old World. They include some root climbers (*Freycinetia*). They are chiefly forest margin or seashore plants. The Typhaceae (*Typha*, 9 sp.) are widely dispersed marsh plants, while the Sparganiaceae (*Sparganium*, 9 sp.) are also water or marsh forms. Both *Typha* and *Sparganium* go back to the Cretaceous. The whole of this primitive order is, therefore, at the present time, confined to primitive types of habitat.

HELOBIEAE. This large order is also generally considered primitive and is largely aquatic with a few marsh forms. Many of the genera are very widely distributed. The Naiadaceae (*Naias*, 30 sp.) have the simplest flowers, but are very likely reduced types. The Alismataceae (12 gen., 75 sp.) are considered by many to be the most primitive since they come nearest, in many respects, to the Ranales. The Potamogetonaceae (9 gen., 100 sp.) are interesting because 8 out of the 9 genera occupy salt or brackish water. The largest genus, however, *Potamogeton*, with 90 sp. is chiefly a freshwater type. Of the Hydrocharitaceae (15 gen., 65 sp.), 3 genera, *Halophila*, *Enhalus*, and *Thalassia*, are marine. The Scheuchzeriaceae or Junca-ginaceae (5 gen., 15 sp.) include the genus *Lilaea*, which has a grass-like habit, a caryopsis type of fruit, and the root of the embryo lateral, suggesting in some of its features the grasses, though in others it is remote from that group. It is a North and South American mountain marsh type. Other families of the order are the Aponogetonaceae (*Aponogeton*, 20 sp.) and the Butomaceae (4 gen., 7 sp.). All the Helobiae in their general wide dispersal show how marsh and aquatic forms are largely independent of climatic conditions.

TRIURIDALES. This order includes only the Triuridaceae (2 gen., 25 sp.), a family of Saprophytes found in the tropics, representing another example of response to the influence of the biota.

GLUMIFLORAE. Only the more important points regarding this order will be mentioned here since it is proposed to deal in detail with the important question of the origin and development of the grasses and grasslands in a subsequent chapter. It is significant that the relatively primitive Cyperaceae (77 gen., 3000 sp.) are mostly marsh forms, though it does not follow that they gave rise to the other family, the Gramineae. The Cyperaceae include one woody tropical genus *Schoenodendron* which has a perianth of scales. On the whole, the tropical Cyperaceae, of which the large genus *Cyperus* is representative, with many florets in the spikelet, are relatively primitive, but the family shows early response to temperate conditions in forms like *Macrochaetium* and *Tetraria*, which occur on the mountains of temperate South Africa and in Australia. The South African genus *Schoenoxiphium* is looked upon as the ancestral form of the Cariceae, in which the genus *Carex* has spread all over the temperate regions of the world. The temperate Cyperaceae, then, afford still another example of a probable mountain origin for the temperate flora.

The evolutionary history of the Gramineae (400 gen., 4000 sp.) has apparently followed somewhat similar lines. The Bamboos

floristically are undoubtedly relatively primitive, and they have a tropical or subtropical distribution, being largely forest margin types and woody. Marsh forms like the Arundineae (*Arundo* and *Phragmites*), which are said to go back to the Cretaceous, may also be reckoned rather primitive. Early response to temperate conditions on mountain ranges is shown by the tribes Aveneae and Festuceae with many florets in the spikelets. Reduction in the number of florets goes hand in hand with increased adaptation to drier conditions or colder conditions in subtropical regions and in temperate steppe regions or in the moorland types, etc. in the tribes Andropogoneae, Paniceae, Stipeae, Agrostaeae, Zoysieae, Sporoboleae, Chlorideae and Hordeae. The relationship of the tribes, and the detailed course of their probable ecological evolution will be discussed more fully later.

The history of the Glumiflorae illustrates our general theory of response to increasing aridity and lower temperatures exceedingly well in all its details.

PRINCIPES. The Palmae (169 gen., 1200 sp.) have a more definite and reliable fossil record than almost any other group of flowering plants, leaves, fruits and well preserved wood, being found as far back as the Cretaceous in north temperate regions, including Great Britain, far beyond their present range. At present the palms are tropical or subtropical. Like the screw pines probably the most primitive were hygrophilous. Many still grow in tropical swamps and rain forest regions or along river-banks (e.g. species of *Nipa*, *Bactris*, *Phoenix*, *Elaeis*, etc.). Others are very distinctly adapted to dry or even semi-desert regions. The Rattans or Cane palms are climbing forms. Some climb by means of prickles, e.g. *Calamus*, a large genus with nearly 300 species. But thorn development is not confined to the climbing forms. It occurs on the stems and leaves and in the case of *Iriartea* even on the roots. While thorn development, almost universally among the Angiosperms, increases with increasing aridity, some of the palms are apparently exceptions to this general rule. Thorns occur in mesophytic or even hygrophilous tropical rain forest types which do not climb, e.g. *Bactris* and *Astrocaryum*, two tropical South American forms. These facts are important in connection with the ecological evolutionary history of plant forms, which will be discussed more fully later. The exact significance of thorn development is a problem which cannot yet be said to have been satisfactorily solved.

SYNANTHAE, Cyclanthaceae (6 gen., 45 sp.). This small order

and family are tropical American and derivative, reflecting, like many of the palms, the influence of the biota. They are plants of palm-like habit, shrubs, climbers, rhizomatous herbs or epiphytes.

SPATHIFLORAE. This order, which is also allied to the Palmae, consists of two families, Araceae (115 gen., 1100 sp.) and Lemnaceae (3 gen., 25 sp.). The Araceae are predominantly tropical and sub-tropical with a few extensions as forest undergrowth or in moist places through the temperate regions. They consist of climbing shrubs or epiphytes, large or small herbs, often with underground rhizomes or tubers. They are another derivative family in response to the tropical biota and show different stages of ecological differentiation. The climbing shrubs are less specialised than the epiphytes and the herbaceous terrestrial forms are, in many respects, the most evolved of all (cf. Bromeliaceae). They are common around the forest margins or in marshy places in the tropics. Colonisation through hygrophilous habitats has extended into the temperate regions. The genus *Arum* has 15 species in the Mediterranean region and central Europe. *Acorus gramineus* occurs in Japan and the sweet-flag (*Acorus calamus*) is widely dispersed through the northern hemisphere. *Calla palustris* is a marsh plant of Europe, Siberia and North America, while the "Arum Lily" (*Zantedeschia aethiopica*) is common all over South Africa. One species, *Pistia stratiotes*, is a widely dispersed aquatic.

The Lemnaceae (*Lemna*, *Spirodela* and *Wolffia*) are the most reduced of all Angiosperms, small, free-floating, thalloid aquatics. *Wolffia* is the smallest Angiosperm, being little more than one millimetre long and having no vascular tissue. The Lemnaceae are found everywhere except in the arctic zone.

LILIIFLORAE. The Juncaceae (8 gen., 280 sp.), a family of marsh plants of wide dispersal are considered by some to show affinities with the Palmae. Many, though they grow in wet places, are xeromorphic. The interesting South African monotype, *Prionium palmita*, is woody (cf. *Schoenodendron* among the Cyperaceae and the Bamboos among the grasses). Certain other small and rather specialised families of the order are tropical and have responded chiefly to the effects of the biota. The Stemonaceae (3 gen., 12 sp.) are herbs, often climbing with flower-parts in fours and a unilocular ovary of two carpels with one anatropous ovule—obviously a highly evolved family. They occur in the East Indies, Australia and America. The Taccaceae (2 gen., 16 sp.) are tropical, mostly Asiatic and American herbs with tubers. The Dioscoreaceae (10 gen., 240 sp.) are climbing

shrubs or herbs with underground tubers or rhizomes, mostly tropical but extending into drier and colder regions, e.g. *Testudinaria* in South Africa and *Tamus communis* in Britain.

All the other families of the Liliiflorae might very well be grouped into a single family. They include the Liliaceae (228 gen., 2600 sp.), the Amaryllidaceae (83 gen., 850 sp.) and the Iridaceae (60 gen., 1100 sp.) together with the Velloziaceae (2 gen., 70 sp.) and the Haemodoraceae (9 gen., 30 sp.). There are a few tree forms (*Dracaena*, *Yucca*) which are subtropical. The great African genus *Aloe* is adapted to xerophytic conditions. There are several climbers (e.g. *Smilax*, *Gloriosa*, many species of *Asparagus*). Some are marsh forms (e.g. *Kniphofia*) and there are many forest margin types as well (e.g. *Clivia*). But the vast majority are geophytes adapted to open grassland or drier subtropical conditions and extending all over the temperate regions as well. Many of the genera are large and widespread (e.g. *Scilla*). Among the Iridaceae, it is interesting to note that probably the most primitive tribe, the Aristinae, have their chief centre of distribution in the Cape mountains with two outside genera (*Eleutherine* in South America and *Orthosanthes* in Australia) another indication that the mountain ranges of the world saw the beginnings of the derivative temperate flora.

Farinosae. The Eriocaulaceae (9 gen., 570 sp.) are a relatively primitive family in this order and are restricted, for the most part, to the warmer regions of the world, their chief centre being tropical America. They have a few extensions into temperate regions and show some connections with the Restionaceae. The Restionaceae (23 gen., 250 sp.) are mostly South African and Australian with a few in New Zealand, Chile, and Cochin China, a family again illustrating the earlier beginnings of a southern temperate flora. Many are marsh forms. Other small families, mostly of marsh plants are the Centrolepidaceae (7 gen., 40 sp.) found in Australia, South America, South-East Asia and Polynesia, the Mayacaceae (*Mayaca*, 7 sp.), American, the Xyridaceae (2 gen., 55 sp.) tropical and subtropical, especially mountainous. The Commelinaceae (29 gen., 320 sp.) are mostly forest margin, marsh or ruderal types in tropical and subtropical regions. The Pontederiaceae (6 gen., 20 sp.) are herbaceous water plants while the Cyanastraceae (*Cyanastrum*, 5 sp.) are an allied small group of tropical African herbs. The Philydraceae (3 gen., 4 sp.) are also herbs distributed from Indo-Malaya to Australia. The Bromeliaceae (57 gen., 920 sp.) are the largest family. The majority are tropical epiphytes, but a few occur on rocks, and two small allied

families Thurniaceae (*Thurnia*, 2 sp.) and the Rapateaceae (7 gen., 25 sp.) are tropical South American herbs. The question as to whether many forest herbs may not have had an epiphytic ancestry is worth considering. Recently Goebel (1922) has described velamen on the roots of various terrestrial orchids as well as on *Agapanthus umbellatus*, *Aspidistra elatior*, *Crinum longifolium*, *Clivia nobilis*, all more or less forest margin types. Velamen also occurs on the roots of grassland terrestrial species of *Eulophia* in South Africa. A typically epiphytic family like the Bromeliaceae, may be more primitive than allied terrestrial herbaceous families. Apart from their mealy endosperm, the Bromeliaceae come fairly near to the Juncaceae among the Liliiflorae, and therefore, may be considered floristically to be rather primitive. Ecologically they are specialised, but epiphytism, like the climbing habit, from which it may often have resulted, may very well have appeared very early in the evolutionary history of the Angiosperms in response to the effects of plant competition and the organic environment (biota) generally. It may be remarked in passing that the terrestrial pineapple (*Ananas*) belongs to the tribe Bromelieae, showing advance in having the ovary inferior, while the other tribes of the Bromeliaceae have the ovary more or less superior.

SCITAMINEAE. This order includes four families with zygomorphic or asymmetrical rather highly modified flowers. They show a tendency towards suppression in the androecium. They are mostly tropical and subtropical plants of the forest undergrowth, forest margins, marshy places or occasionally fairly xerophytic situations which, in their floral structure, as well as ecologically, show response to the influence of the biota (including not only the insect world but, in many cases, birds as well). The Musaceae (6 gen., 58 sp.) approach nearest to the ordinary monocotyledonous type of flower. They are mostly perennial herbs, often large (*Musa*, *Strelitzia*) but some are woody (e.g. *Ravenala*, the Traveller's Tree of Madagascar). The Zingiberaceae (41 gen., 900 sp.) or ginger family are perennial herbs with elongated or tuber-like rhizomes and often thickened roots. Schumann, who dealt with them in Engler's *Pflanzenreich* (1904) points out their similarity in many vegetative characters to the Gramineae and Sargent and Arber (1915) also find affinities in the seedling anatomy of gingers and grasses. The Cannaceae include only the genus *Canna* with 40 species in the warmer parts of America. The Marantaceae (27 gen., 290 sp.) have the flowers most modified of all. They belong chiefly to the American tropics.

MICROSPERMAE. This highly specialised order includes the Burmanniaceae (18 gen., 60 sp.) a family of tropical forest herbs, mostly saprophytes or, in a few cases, root parasites and the Orchidaceae (500 gen., 7500 sp.). The Orchidaceae are a large family of subordinate forms, some entirely dependent as epiphytes or saprophytes, the others dependent as associated plants. The orchids, though numerous in point of species, are never dominant and ecologically cannot be described as a successful family, since they always play a subordinate rôle in vegetation.

The epiphytic forms are highly evolved as epiphytes, though their origin may be more ancient than the terrestrial forms. The latter, as we have seen, in some cases have velamen, which may indicate that they had an epiphytic ancestry. Comparison of flower structure, however, in the terrestrial and epiphytic forms gives no certain indication of what the course of their evolutionary history has been. All the Microspermae show in the highest degree the effects of the biota and their complex evolutionary history is a very difficult one to disentangle.

SUMMARY

1. The Sympetalae are doubtless of polyphyletic origin and certain of their groups may be more ancient than many of the Archichlamydeae, yet, in a general way, the Sympetalae are recognised as highly evolved. It is significant, therefore, that they are, on the whole, adapted to colder and drier conditions, or in the moist tropical regions are mostly subordinate types, showing response to the influence of the organic environment or biota.

2. Several of their important groups (as among the Archichlamydeae) indicate a mountain origin for the temperate flora, e.g. the Ericaceae and other families of the Ericales, temperate members of the Verbenaceae, temperate families of the Rubiales and Campanulatae including the highest family of flowering plants, the Compositae.

3. Whatever the actual origin of the Monocotyledons may have been, all the available evidence points strongly in the direction of the earlier forms having been hygrophilous, forest margin or marsh types. Such types, at the present time, as doubtless in the past, tend to become very widespread and are relatively unaffected by climatic differentiation. On the whole, therefore, their present geographical distribution does not throw quite so much light on the ecological history of the Monocotyledons as is the case with the Dicotyledons. Nevertheless, here also the influence of the biota under moist tropical

conditions has led to the production of advanced specialised types and, in general, climatic differentiation has had an effect. The more advanced types are those which have responded to drier conditions on the one hand, and colder conditions on the other.

4. There are certain indications in the families Araceae and Bromeliaceae, that terrestrial forms may have been derived from epiphytic ancestors. The order of evolutionary development in these cases in response to the biota would be climbing forms—epiphytes—terrestrial herbs. The evidence, however, is not sufficient to enable us to argue that many herbs originated in this way.

5. The detailed evidence among the Sympetalae in support of our general theory is best summarised in the form of a table as in chapter II for the Archichlamydeae.

COMPARATIVE TABLE FOR SYMPETALAE

Systematic position	Relatively primitive, tropical or subtropical, hygrophilous or mesophytic	Relatively advanced, more temperate or more xerophytic
1. Dicotyledons	Rutales	Ericales
2. Primulales	Myrsinaceae	Primulaceae
3. Myrsinaceae	<i>Embelia</i>	<i>Maesa</i>
4. Sympetalae	Primulales	Plumbaginaceae
5. Sapotaceae	Tropical genera	<i>Mimusops, Sideroxylon</i>
6. Ebenaceae	Tropical genera	<i>Euclea, Royena</i>
7. Oleaceae	Subtropical genera	<i>Fraxinus</i>
8. Contortae	Loganiaceae	Gentianaceae
9. Contortae	Loganiaceae	Asclepiadaceae
10. Contortae	Apocynaceae	Asclepiadaceae
11. Loganiaceae	Loganioidae	Buddleioideae
12. Asclepiadaceae	Periplocoideae	Other tribes
13. Asclepiadaceae	Other tribes	Stapeliae
14. Convolvulaceae	Tropical woody genera	Herbaceous genera
15. Convolvulaceae	Tropical woody genera	<i>Cuscuta</i>
16. Personales	Solanaceae	Scrophulariaceae
17. Personales	Verbasceae	Scrophulariaceae
18. Scrophulariaceae	Tropical trees	Herbaceous genera
19. Bignoniacae	Tropical trees	<i>Rhigozum</i>
20. Personales	Bignoniacae	Pedaliaceae, Martyniaceae
21. Acanthaceae	Mendonsioideae } Thunbergioideae }	Acanthoideae
22. Lamiales	Boraginaceae	Labiatae
23. Boraginaceae	Cordioideae } Ehretioideae } Heliotropoideae }	Borraginoideae
24. Verbenaceae	Tropical forms	Temperate forms
25. Lamiales	Verbenaceae	Phrymaceae
26. Sympetalae	Personales	Plantaginales
27. Rubiales	Rubiaceae	Other families
28. Rubiaceae	Cinchonoideae	Coffeoideae
29. Rubiaceae	Woody genera	Herbaceous genera
30. Rubiaceae	Other tribes	Galieae
31. Dicotyledons	Other families	Compositae

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(To be continued.)

RAPID CONDUCTION OF STIMULI IN *MIMOSA PUDICA*

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INTRODUCTION

A DIVERSITY of opinions still exists as to the mechanism by which stimuli are transported in the stems and leaves of *Mimosa pudica* and *Mimosa Specazzinii*. The work of Ricca(6), which has

been confirmed by Snow(10), Seidel(9) and also by the writer(1), has proved the possibility of transport through the movement of a chemical stimulant by water currents in the xylem.

In spite of the evidence to the contrary which has been adduced, Bose prefers to regard the transmission of stimuli in *Mimosa* as due entirely to the propagation of protoplasmic excitation, and rejects all theories based on water movement. The work which he has done on this subject and the theories which he has put forward have been summarised in his recent book(2).

Snow(10) has accepted the view of Ricca that normal transmission in the stem is due to a hormone travelling in the xylem, but concludes that there is, in addition, a peculiar "high-speed" conduction which he presumes to travel either in the phloem or in the cambium. With regard to the leaf, he considers that the path of conduction is in the phloem, and that transmission, at any rate in the basipetal direction, does not depend on the movements of the water current.

Seidel(9) is also a supporter of the view that there is more than one method of conduction. He regards one as taking place by the transport of a hormone, and the other by pressure changes in the "tube-cells" of the phloem, as advocated originally by Haberlandt(5).

Of the various theories which have been propounded from time to time, the one which appears to conform most closely to the available evidence is that of Ricca, but certain facts make it extremely doubtful if his theory can be regarded as a complete explanation of all aspects of this difficult problem.

RAPID CONDUCTION IN SUBMERGED SHOOTS

Certain preliminary experiments having shown that a very rapid conduction of stimulation could occur in shoots which had been submerged in water for some hours, it was decided to investigate the matter more fully, with the object of determining whether such cases of conduction could be explained according to Ricca's hypothesis. At first it was thought that the conduction which occurred under such conditions was identical with the "high-speed" conduction described by Snow(10). Snow found that in several cases where cuts were made with a razor into the phloem, the leaf next above the wound fell almost instantaneously. The leaflets did not close nor did the excitation reach any other leaves.

An apparently similar case of high-speed conduction was obtained by Snow in the case of a submerged shoot which had been in

water for three hours. The base of the shoot was cut off and the first two leaves of the stem fell almost instantaneously, but their leaflets did not close.

According to the writer's experience, conduction in a submerged shoot is not as a rule limited to a few leaves but passes right along the shoot with a velocity which usually varies from 100 to 200 cm. per minute. For the sake of clearness, it is proposed in this paper to allude to this form of conduction as "rapid" conduction, in contrast on the one hand to the "normal" conduction elucidated by Ricca, and on the other, to the "high-speed" conduction described by Snow. The question of the relationships of these types of conduction to one another will be discussed later.

EXPERIMENTAL METHODS

Ample material of *Mimosa pudica* was available from plants which were growing on some waste ground beside the laboratory. The shoots were cut under water and placed with their cut ends in a vessel of water. They were then brought into the laboratory and completely submerged. Any necessary operations were performed under water. The shoots were then laid horizontally in water in large glass dishes which were placed on a bench in front of a window. It was found to be important that they should be exposed to a bright light, but direct sunlight was avoided. On several occasions when the sky was darkened by heavy clouds the shoots became more or less insensitive.

Weights were laid on the stems to keep them in place, and the shoots were allowed to rest for at least two hours before being tested. The velocity of conduction of the stimulus was timed by a stop-watch, or in some cases, by a metronome. No very high degree of accuracy can be obtained by this method, but this is not of any great importance, as there is a fairly large variation in velocity in individual shoots and even during the passage of the stimulus along a single shoot.

THE EFFECT OF DECORTICATION

Ten shoots were submerged in water. In five of the shoots a zone of cortex about 1 cm. wide was stripped off from an internode in the middle of the shoot, and then all the remaining tissues of this zone external to the wood were carefully dissected away. The surface of the wood was scraped clean with the blade of a knife. The other five shoots were left intact.

The ten shoots were laid in water in dishes, as already described, and were left undisturbed for three hours. Each shoot was then

stimulated in turn by cutting off the apex with a pair of scissors, the cut being made 2 or 3 cm. from the extreme tip. Previous experiments had demonstrated that rapid transport of the stimulus can be initiated by cutting either the apex or base of the shoot, but to avoid the risk of jarring the shoot, it is preferable to make the cut through the softer tissues at the apex.

With the exception of one case, in which only the first leaf below the cut was affected, the stimulus passed regularly along the shoots. In one or two cases a leaf moved a moment before the one at the node behind, but in the great majority the pulvini reacted in strict succession. In about half the shoots the basal petiole did not move, but otherwise the stimulus travelled right along, affecting every leaf. The temperature was about 30° C.

TABLE I

Intact Shoots			Ringed Shoots		
No. of shoot	Extent of transmission (cm.)	Velocity, cm. per sec.	No. of shoot	Extent of transmission (cm.)	Velocity, cm. per sec.
1	—	—	2	1.4	2.8
3	2.2	3.7	4	2.3	3.3
5	2.6	3.2	6	20.5	2.9
7	1.7	3.4	8	1.4	2.8
9	2.1	3.5	10	1.7	3.1
Mean 3.45			Mean 3.0		

The velocities obtained in this experiment (Table I) were slightly above the average (2-2.5 cm. per sec.) usually obtained in submerged shoots. The difference between the ringed and intact shoots has probably no significance and may be attributed to individual variation. So far as could be observed, no diminution in velocity occurred as the stimulus traversed an internode containing a decorticated zone.

In this experiment the decorticated zone was only about 1 cm. wide in each of the shoots, but on another occasion the effect of varying the extent of the decortication was investigated. Eighteen shoots were used, each about 35 cm. in length. All the tissues external to the wood were removed in a zone 1, 2, 3 or 4 cm. in length in an internode in the middle of each shoot. In two other shoots, what had unusually long internodes, the decorticated zones were 6 cm. in length. The experimental arrangements were the same as in the last experiment. In several cases the shoots were more or less insensitive and either no leaves moved or else only the one or two which were nearest the point of stimulation. In those shoots where

the stimulus traversed the decortication, the velocities were as shown in Table II.

TABLE II

Length of decorticated zone	1 cm.	2 cm.	3 cm.	4 cm.	6 cm.
Velocity of transmission in cm. per sec.	2.3	2.6	—	3.0	2.1
	2.2	2.7	2.4	2.7	—
	2.6	—	2.4	2.4	—
Mean velocity	2.4	2.65	2.4	2.6	2.1

There is therefore no correlation between the velocity of transmission and the length of the decorticated zone.

During this experiment the velocities of transmission in the decorticated internodes were noted in a number of cases and were of the same order as those in the intact internodes. For example, in the shoot in which the tissues outside the wood had been removed for a distance of 6 cm., the stimulus passed across the decorticated internode, 7 cm. in length, with a velocity of 2.0 cm. per sec. This is approximately the same as the velocity recorded above which was measured over about three internodes, a distance of 19 cm.

Other methods of stimulation were also used. A shoot was decorticated as before and almost entirely submerged, the apex alone being allowed to project from the water. After a period of rest, the protruding apex was burnt with the flame of a match. The stimulus passed along the shoot, traversing the decorticated zone. The time taken for the stimulus to pass from the first to the sixth leaf, a distance of 18 cm., was 8 secs., giving a velocity of 2.2 cm. per sec.

Electrical stimulation was also employed. Copper wire electrodes were attached either in the same internode or in the next internode to the decorticated zone. After the shoots had been allowed to rest under water for some hours, each was subjected to a single strong electric shock from an induction coil. In several cases the stimulus passed beyond the decorticated zone, the velocity of transmission varying from 1.6 to 2.0 cm. per sec.

It is thus clearly established that a rapid conduction of stimulation can take place in submerged shoots. In every case where successful transmission past a decorticated zone was observed, the completeness of the removal of all tissues external to the wood was confirmed microscopically at the close of the experiment. There is no doubt, therefore, that the phloem and cortical tissues are not essential for the transport of the stimulus in the stem, and their

presence or absence seems to have no influence on the velocity of transmission. This fact proves that rapid conduction can take place quite apart from the mechanism advocated by Haberlandt (5), which involves the tube cells in the phloem.

In some respects this rapid form of conduction bears a certain similarity to the "high-speed" conduction described by Snow. In both cases the movements are confined to the main pulvini. In the experiments which have been described, the leaves were for the most part fully expanded and usually floated on the surface of the water. When these leaves reacted the leaflets almost always remained expanded, but occasionally a few leaflets closed. This appeared to be due to direct stimulation while the leaf was being dragged through the water by the movement of the main pulvinus.

Great stress is laid by Snow (10) on the non-closure of the leaflets as a criterion of "high-speed" as distinct from "normal" conduction. This condition is fulfilled, not only in the case of "rapid" conduction in submerged shoots, but also (as will be described later) in highly turgid aerial shoots.

Since the tissues external to the wood appear to play no part in the mechanism of rapid conduction, it is necessary to consider the function of the remaining tissues.

THE POSSIBLE FUNCTIONS OF THE WOOD IN RAPID CONDUCTION

In spite of the objections advanced by Bose, the function of the wood in permitting normal conduction by the transport of a hormone in the water current seems to be well established. This theory presupposes the existence of tension in the water in the tracheae. It is well known that the velocity of the conduction depends largely upon the amount of tension existing at the time, being much greater on a dry day when the tension is high. Snow (10) found that the velocity in growing shoots was from 10 to 15 cm. per minute. In damp weather it was very much less. In my own experiments, speeds up to 28.5 cm. per minute have been obtained as a result of normal conduction in dry weather, but the average is usually considerably smaller. Such velocities are evidently of quite a different order from those obtained in submerged shoots. In the latter, at the temperature of my experiments (27-30° C.), the stimulus is often transmitted through considerable distances at a speed of over 200 cm. per minute. For such a velocity to be due to water movement would necessitate the existence of a very high tension. Although it appeared extremely improbable that such a condition could be realised in the case of

shoots which had been submerged in water for some hours, the possibility could not be entirely ignored.

(i) *The existence of tension in the tracheae of submerged shoots.*

It has long been known that a transpiration current occurs in submerged plants or parts of plants. This is regarded by Dixon⁽³⁾ as due to the secretion of water by the living cells of the leaves. The existence of a transpiration current in the case of submerged shoots of *Mimosa* was proved as follows: A potometer with a horizontal graduated tube was connected by means of a bent glass tube to a submerged shoot which was lying in a dish of water. The capillary tube of the potometer was arranged so as to be at the same level as the surface of the water in the dish. In the case of a shoot about 30 cm. long, bearing seven leaves, the rate of absorption of water, after the shoot had been submerged for three hours, was 0.013 c.c. per hour.

Another method of estimating the tension in submerged shoots is to cut them under stain. The shoots were first defoliated by cutting off the leaf blades under water, the cut being made near the apex of each petiole. This operation has little or no effect on the transmission of stimuli, but renders the shoots easier to handle. The shoots were submerged in water for three hours and were then carefully removed, one at a time, and the apex immersed in 5 per cent. eosin solution. The top of the shoot was cut off with a pair of scissors below the surface of the stain. The time taken for the stimulus to pass along the shoot was noted and the apex was then removed from the stain and rinsed in water. Transverse sections were immediately cut with a dry razor in order to determine the extent through which the stain had travelled. In the case of insensitive shoots the apex was allowed to remain in the stain for 30 secs.

TABLE III

No. of shoot	Distance traversed by stimulus (cm.)	Time (secs.)	Velocity, cm. per sec.	Distance traversed by stain (cm.)
1	21.5	8	2.7	6.5
2	Insensitive	—	—	2.5
3	19	5	3.8	3.2
4	Insensitive	—	—	2.0
5	16	4.5	3.5	4.0

The distance traversed by the stain, as recorded in Table III, is the extreme limit at which the effect of the stain could be detected. The stain was not equally distributed in the wood except close to the

cut. At a little distance from the cut it was confined to only a few of the vascular bundles and persisted longest in one or two of the larger vessels. The existence of tension in these submerged shoots cannot be denied, but there is a very marked difference between the distance traversed by the stain and the distance traversed by the stimulus in the same period of time.

(ii) *The effect of prolonged immersion.*

If the rapid propagation of the stimulus in submerged shoots depended upon tension in the water in the tracheae, it appeared probable that the velocity of transport would be decreased in shoots which had been submerged in water for a long time. In order to test this point, numerous shoots were collected and the leaf blades cut off under water through the upper part of each petiole. Water was thus free to enter the shoots at the base and through each of the cut petioles. The shoots were submerged in water and left for different lengths of time before being tested. In one set of experiments the apex of each shoot was allowed to project from the water and stimulation was effected by applying a flame to the protruding apex. In the other set of experiments, which were performed on the next day, the shoots were entirely immersed and were stimulated by cutting off the apex with a pair of scissors. The velocities were only recorded in cases where the stimulus passed through a distance of over 10 cm. The remaining shoots either failed to conduct or did not transmit the stimulus beyond the first or second leaf. The temperature was 27–28° C. The velocities given in Table IV are in cm. per sec.

TABLE IV

Time submerged	1 hr.	1½ hrs.	2 hrs.	3 hrs.	4 hrs.	5 hrs.	6 hrs.	7 hrs.
Burn-stimulus	—	—	—	1.5	1.5	0.6	—	2.0
	—	1.2	2.2	—	0.7	1.7	2.0	—
	0.8	—	—	—	1.4	1.6	1.7	2.9
Cut-stimulus	0.6	—	1.9	2.3	2.3	2.9	2.3	2.7
	—	2.0	2.0	?	—	2.4	2.5	2.9
	2.2	2.3	—	2.6	2.8	2.2	2.2	2.4

These figures indicate the results obtained from tests on 48 different shoots which had been submerged for the times stated. They show that submergence in water, although this would tend to lower the tension, does not decrease the velocity of transmission. If anything, there is a tendency for the velocity to increase after the shoot has been submerged for some hours. The four values of

less than 1 cm. per sec. were due to the fact that a considerable pause occurred after the stimulus had been applied before transmission commenced. In those cases where the shoots were stimulated by a flame, the time was taken from the moment when the flame was applied. Owing to the delay which occurs before the effect of the flame reaches the inner tissues, the velocities appear to be slightly lower than those obtained as the result of a cut. In many of the shoots the stimulus reached the last pulvinus, which, in one case, was only 7 mm. from the base.

The shoots which had been used in these experiments were left submerged overnight and then tested. The majority were insensitive, but in six cases, velocities varying from 1.1 to 1.9 cm. per sec. were obtained over an average distance of 15 cm. The stimulus was either a cut or a burn.

Defoliated shoots which have been submerged in water for 24 hours can therefore conduct stimulation with considerable velocity, a fact which strongly opposes the idea that tension can be the cause of the transport.

(iii) *The possibility of transport by the wood alone.*

If rapid conduction could be explained by the movement of water in the tracheae, it should be possible for the stimulus to traverse a part of the stem in which all the living tissues have been removed or killed. It should also be able to pass through a water-filled tube from one half of a shoot to the other. These possibilities were investigated.

(a) *Removal of living tissues.* Fourteen shoots were decorticated in the usual way for a distance of 2.5 cm. in a middle internode. While still under water, the wood was cut away from the upper side so as to expose the pith for about 1.5 cm. in each decorticated zone. The pith was then scraped out with a little brush made of fine wires, the depithed zone being 7-10 mm. long. In this way the tissues internal and external to the wood were removed, but about half of the woody cylinder was left as a gutter-shaped connection between the two halves of the shoot. Six of the shoots were leafy, but in the other 8 the leaf blades were cut off at the tops of the petioles. The shoots were allowed to rest under water for three hours and then the apex of each was cut off. In 7 out of 14 shoots (3 leafy and 4 defoliated), the stimulus passed as far as the pulvinus next to the decorticated zone. The velocities varied from 1.3 to 2.6 cm. per sec. over distances of 10-14.6 cm. The other shoots were insensitive, or else showed movement in only a few leaves. In no case did the

stimulus cross the decorticated and depithed zone. After a further rest of one hour, the shoots were divided into two by a cut across the wood in the middle of the depithed zone. This operation did not cause stimulation in a single case. Cuts were then made in the decorticated parts of the half-shoots about 5 mm. from the original cuts. This time some of the pith was included in the cut. Out of 15 tests, 11 gave positive results, the stimulus passing through several internodes at the ordinary rapid rate.

In so far as negative evidence can be considered valid, these experiments show that the wood alone can neither initiate nor transmit rapid conduction. It is, however, certain that wood and pith combined are able to do so.

(b) *Destruction of living tissues by steam.* Experiments were also carried out to determine whether rapid conduction could pass through a portion of a stem which had been killed by means of steam. The shoots were first submerged in water for some time so that they might become fully turgid. Then, in order that there should be no doubt as to the killing of the inner tissues, they were decorticated for a distance of 5-10 mm. in a middle internode. In each case the decorticated zone was rotated in a steam jet for two minutes, the neighbouring parts of the stem being protected with wet cotton wool. After the shoots had been allowed to rest under water for three hours, they were stimulated by cutting or burning the tips, which, in the latter case, projected from the water. In 6 cases out of 16 the stimulus passed as far as the steamed zone, but did not cross it. In 5 others, several of the leaves moved but the one next to the zone did not. The remaining shoots showed no transport.

In 2 cases out of 7, where the stimulating cut was made very close to the steamed zone, the stimulus traversed this zone. In 1 case the cut was made in the next internode on the apical side. The pulvinus between the cut and the zone reacted after about 1 sec., and the next pulvinus *beyond* the zone moved 2 or 3 secs. later. In the other successful experiment, the cut was made in the same internode as the steamed zone. The pulvinus beyond the zone contracted almost simultaneously. The greatest care was taken to avoid jarring, and in these two experiments it appeared to be certain that the reaction of the pulvini was not due to this cause, but to the passage of the stimulus across the killed zone. The significance of these results will be discussed later.

(c) *Effect of a discontinuity.* The passage of a stimulus through a water-filled tube has provided definite proof that "normal" conduction

in *Mimosa* is effected by water movement, and not by the propagation of a nervous impulse. By the use of this test it was hoped to obtain definite evidence as to the mechanism of "rapid" conduction.

Shoots were cut across under water and the ends fitted into a short piece of water-filled rubber tubing, which fitted tightly, the two cut surfaces being brought very close together. The ends of the tube were firmly bound with thread. After a rest of some hours under water, the shoots were stimulated by cutting off the apex of each, or by squeezing the apex or base with a pair of forceps. In a few cases, the apex, which was allowed to project from the water, was stimulated by a burn. The experiment was repeated a large number of times and on different occasions.

The results of 80 tests were as follows: In 19, the shoots failed to conduct the stimulus in any part; in 23, only a few leaves close to the point of stimulation reacted, while in 38, the stimulus was transported as far as the discontinuity. In no case did the stimulus, after having passed along the shoot, traverse the discontinuity.

The result was very often different when the stimulus was applied close to the rubber tube connecting the two halves of the shoot. Out of 5 experiments in which the stimulating cut was made in the internode next to that containing the discontinuity, the stimulus, on 3 occasions, traversed the gap and affected one or more pulvini on the far side. Stimulation was also carried out by cutting the stem, or by squeezing it with a pair of forceps in the same internode as the discontinuity. In 9 out of 40 tests the stimulus passed across the gap. For example, in one experiment, the stem was cut across with a pair of scissors about 1 cm. from the discontinuity. The three leaves on the far side reacted in turn, the third, which was 8 cm. from the point of stimulation, moving after 4 secs. Similar results were obtained in other cases but sometimes only the first pulvinus beyond the discontinuity reacted, the movement taking place almost immediately after the stimulus was applied. It is absolutely certain that in the great majority of the experiments recorded above, and probably in all, the contraction of the pulvini on the far side of the discontinuity was not due to jarring of the shoot. On a few occasions jarring did occur, and was marked by the simultaneous movement of all or most of the leaves. The results of such experiments were rejected. At one time it appeared conceivable that transference of the stimulus across the gap could be effected by the two cut surfaces rubbing against one another as the shoot was stimulated. It was, however, proved by direct experiment, that stimulation of one

half of the shoot by the other could not be brought about in this way.

It seems reasonably certain that in cases where stimulation has been transmitted for some distance in a submerged shoot, the stimulus is unable to pass through a killed zone or to traverse a discontinuity. In the latter case this result might conceivably have been due to blocking of the tracheae, and various precautions were taken to minimise this possibility. In many of the experiments, the tissues external to the wood were first removed for a short distance at the point where the shoot was cut in two, the object being to avoid forcing the contents of the phloem cells into the tracheae as the shoot was severed. In other cases, the air was removed from the inter-cellular spaces after cutting the shoot in two. This precaution was found by the writer (1) to be necessary for obtaining conduction past a discontinuity in the case of aerial shoots where the tension is greater, as the gap between the cut surfaces is readily blocked by bubbles of air which emerge from the intercellular spaces. None of these arrangements seemed to have any effect on the results in submerged shoots, and, when stimulation was carried out close to the discontinuity, several cases of successful transmission were obtained in their absence. It may be assumed, therefore, that they were unnecessary, and that effective blocking did not occur.

The difference between the results according to whether the stimulus is applied some distance away from, or close to, the discontinuity or steamed zone, seems open to explanation. In the former case, as the stimulus passes along the shoot, the movement of water in the tracheae, if it occurs at all, is too slight to enable the stimulus to pass the discontinuity or a killed zone. In the latter, a stimulating hormone is carried across the discontinuity in the drop of liquid which is squeezed out of the tracheae as the cut is made. (The emission of such a drop from the wood at the basal end of a highly turgid cut shoot is easily seen if a second cut is made with a pair of scissors higher up the stem.) A drop of liquid would thus be forced from one half of a shoot to the other if the two were closely connected by a water-filled tube. This would occur no matter whether the cut was some distance away from, or close to, the discontinuity, but in the latter case only, the drop of liquid would contain sap from the injured cells and would therefore set up stimulation in the other half of the shoot.

The experiments which have been described, show that although rapid conduction is not accompanied by an appreciable water current,

it is in some way connected with a hormone mechanism and is not due to the propagation of a nervous impulse.

(d) *Absence of water movement during conduction.* The view that rapid conduction is not accompanied by an appreciable movement of water in the tracheae is also supported by the following evidence. In the experiment previously described where a submerged shoot was connected with a potometer, the meniscus in the capillary tube was carefully observed with a lens during the passage of a stimulus along the shoot. The shoot was stimulated by cutting it across with a pair of scissors about 10 cm. from the apex. As the cut was made, a momentary flattening of the meniscus occurred, due to squeezing of the wood. The stimulus passed from the cut along the remainder of the shoot, a distance of 16 cm., in 6 secs., but during this time the meniscus remained absolutely stationary. It is inconceivable that any appreciable water movement could have occurred while the stimulus traversed the shoot, without causing movement of water in the potometer.

After the stimulus had passed, it was noticed that the rate of absorption of water, as recorded by the potometer, rose for a period of 10 minutes to about twice the normal rate, from 0.013 c.c. per hour to 0.027 c.c. per hour, and then again became normal. This increased rate was probably due to absorption of water by cells which had contracted during the passage of the stimulus.

THE EFFECT OF REMOVAL OF THE PITH ON RAPID CONDUCTION

It has already been pointed out that, in the stems from which the outer tissues have been removed, the wood and pith combined can both initiate, and provide a path for, the rapid conduction of stimuli. The wood alone is unable to do this, although it can be utilised in conduction when a stimulating hormone is forced through it by squeezing the stem.

The problem still remains, as to whether, in the absence of the pith, the wood, combined with external tissues, could permit rapid conduction. To investigate this matter, 12 shoots were chosen which had rather thick stems towards the base. In each basal internode the stem was pared away under water so as to expose the pith for a distance of 3-4 cm. The pith was then completely scraped out in 10 of the shoots. In the other 2 shoots the pith was left intact. The shoots were allowed to remain under water for three hours and were then stimulated by squeezing with a pair of forceps the part which had been operated on.

In no case was stimulation transmitted from the depithed portion, but with regard to the shoots with intact pith, the stimulus was transmitted through four internodes in one case; the other shoot did not conduct.

The shoots were then stimulated by squeezing them just above the part which had been depithed. In 4 shoots, the stimulus passed right along the whole shoot, in 4 others, one or more pulvini reacted, while 2 failed to conduct the stimulus.

The base of each shoot was then withdrawn from the water and covered with wet cotton wool. After the shoots had rested for an hour, the cotton wool was removed, and the depithed regions were burnt in a flame. In no case was the stimulus transmitted, but in both of the shoots with intact pith the same treatment caused the nearest pulvinus to react. A flame applied afterwards to the intact part of the stems just above the depithed portions caused conduction in the majority of cases. The evidence therefore points to the conclusion that the tissues external to the wood play no part in rapid conduction, a conclusion which is confirmed by the fact that rapid conduction appears to be unaffected by the removal of these tissues.

The only living tissue which seems essential is the pith, using the term to comprise all living tissues within the cylinder of wood, and including the elongated cells lying on the inner side of the protoxylem, the "inner phloem" of Bose(2).

Whether the pith can conduct, without the co-operation of the wood, was not determined, as the difficulties of removing, or effectually blocking, the wood, without causing injury to the pith, could not easily be surmounted.

THE MECHANISM OF RAPID CONDUCTION IN THE STEM

In formulating a theory as to the mechanism of rapid conduction, it is necessary to bear in mind that many of the conclusions which have been reached by means of experiments, are based upon negative results, and therefore depend more on the balance of probability than on definite proof. The following points, however, seem to be well established:

1. Rapid conduction takes place under conditions of high turgidity, such as obtain in submerged shoots.

2. It is clearly distinguished from normal conduction, the rate of which depends largely on the tension of the water in the tracheae. Many shoots appear unable to transmit rapid conduction, but if this does occur, the velocity is at least 1 cm. per sec.

3. It is not accompanied by appreciable water movement.
4. It is not due to propagation of nervous impulses.
5. It is not due to pressure changes in the tube cells of the phloem, as advocated by Haberlandt (5), since removal of the phloem is without effect on it.
6. It only occurs in regions of the stem where the pith is wholly, or partially, intact.
7. It affects the main pulvini only, and does not pass out into the leaves.

It is necessary to consider the conditions obtaining in a highly turgid shoot. Every cell will have absorbed water and will have expanded until the inward pressure of the cell wall, either due to its own tension, or to the pressure of the neighbouring cells, is equal to the highest osmotic pressure capable of being exerted by the solutes of the cell sap. The slightest change of permeability, due to any kind of stimulation, will cause the stretched cell wall to contract suddenly, and to expel, under very high pressure, some of the contents of the vacuole. It is known that the cells of *Mimosa* contain a hormone capable of causing contraction of the cells of the pulvinus, and it is probable that the same stimulant will cause a change in the permeability of the living cells of the stem when applied to them.

The stimulant which has been ejected into the intercellular spaces, or into the tracheae (it is uncertain which), will affect neighbouring cells, causing them to collapse in turn, and so the process will go on.

A mechanism such as this could explain how rapid conduction might pass along a turgid shoot, and might be compared to the passage of a flame along a train of gunpowder. The slight tension which may exist in the water in the tracheae, even when the shoots are submerged, may possibly assist in the transport of the hormone, but this tension does not appear to be of any importance and is probably unessential.

The objection might be raised that the mechanism which has been suggested could not explain a sufficiently rapid transport, involving, as it does, the successive contraction of hundreds of minute cells within a short space of time. When one considers, however, the extraordinary rapidity with which the cells of the pulvinus are able to react as a result of stimulation, this objection does not seem to have so much force. What is probably essential is that the cells of the tissue responsible for rapid conduction should have increased their turgor sufficiently to bring them to a state of unstable equilibrium, so that instantaneous contraction is possible.

Ricca(8) has suggested that, "in certain cases at least, the sap expelled from the responding pulvini, containing in all probability the hormone, helps in the propagation of the stimulus." The pulvini would seem to be too far apart to be really effective in this respect, and, moreover, the contraction of a pulvinus is not as a rule sufficient to cause rapid conduction. In a number of cases, one of the pulvini of a submerged shoot was stimulated by a touch on the lower surface. This pulvinus contracted at once, but the stimulus was not transmitted to the other leaves. The stem was then lightly rubbed with the back of a knife close to the stimulated pulvinus. This caused rapid conduction in both directions. Very occasionally, direct stimulation of a pulvinus gave rise to transmission, but in most cases it was found necessary to apply the stimulus to an internode.

The fact that so many shoots appeared incapable of rapid conduction is rather striking. In some cases this was due to insufficient illumination, but in the majority, no definite reason for the fact could be assigned.

The question arises as to the identity or otherwise of the "rapid" conduction, which occurs in turgid shoots, with the "high-speed" conduction described by Snow(10).

This method of conduction is easily obtained by making a very slight cut with a razor in an internode directly below a leaf. It is sufficient to make the cut just deep enough to reach the phloem. A drop of sap exudes from the tube cells, and the leaf above usually falls almost immediately, but sometimes there is a pause of about $\frac{1}{2}$ -1 sec. Occasionally the leaf beyond on the same side also reacts about a second later. In no case did the stimulus affect more than two leaves.

The two kinds of conduction agree in affecting only the main pulvinus, but differ in velocity, and in the fact that whereas "high-speed" conduction is confined to one or two leaves on the same side as the cut, "rapid" conduction may pass along the whole shoot affecting every leaf.

On a number of occasions, shoots were decorticated down to the wood for a short distance in an internode near the base. The decorticated zone was kept moist with wet cotton wool or else kept under water, until the shoot was ready for testing. In two cases the decorticated part was covered with vaseline, the base of the shoot dipping into water. The presence of the decortication invariably prevented the passage of "high-speed" conduction in the internodes.

in which it occurred, although this form of conduction could still be obtained by stimulating the intact internodes with a cut reaching to the phloem. It was noticed that there was no exudation from the tube cells in the decorticated internodes when the phloem was cut. These cells apparently became emptied during the process of decortication and failed to refill.

It seems probable that "high-speed" conduction, unlike "rapid" conduction, is propagated in the phloem, possibly by successive collapse of the tube cells. Snow(10) considers that it travels in the inner part of the phloem or in the cambium, but Dixon(4) has suggested that it is due to the release of tension in one or two tracheae followed by a very rapid movement of sap. If the latter were the case, one would expect it to be more prevalent under conditions of active transpiration. Numerous tests were made on growing plants in damp and in very dry weather and showed that "high-speed" conduction occurred under conditions of either depressed or active transpiration.

With regard to the possibility of "high-speed" conduction in submerged shoots, it was found that if a cut was made into the phloem in a direct line below or above a leaf, this leaf moved immediately. The reaction was not, however, confined to this leaf, but the stimulus passed along the shoot in both directions at the usual rapid rate of 1-3 cm. per sec.

It appears then that "high-speed" conduction can occur equally well in shoots which are transpiring rapidly, and in those which are submerged in water. In the latter case, "rapid" conduction can also occur. It is possible for the two methods of conduction to be initiated by the same stimulus, "high-speed" conduction being limited to one or two leaves, whereas "rapid" conduction has a longer range but a slower velocity.

The evidence in favour of regarding the pith as the tissue mainly responsible for rapid conduction has already been pointed out. The fact that a cut reaching only to the phloem, or even a slight rub on the surface of the stem, is sufficient to start rapid conduction, necessitates a mechanism by which the stimulus can pass from the outer to the inner tissues. The transference of a hormone in the transverse direction through the tracheae would appear to be difficult, and, at any rate, would be a slow process. It is possible, however, that stimulation of the external tissues by a cut or rub might set up sufficient vibration to pass through the wood and excite directly the turgid tissues of the pith. If a cut is made into the phloem exactly

opposite one of the leaves of a growing stem, this leaf as a rule fails to react, but if the same operation is conducted on a submerged shoot, this leaf moves almost immediately and before the ones on either side which are in a direct line with the cut. In the case of the submerged shoot, the stimulus must have passed across the stem, conceivably by means of the phloem, but more probably directly through the wood and pith.

RAPID CONDUCTION IN GROWING PLANTS

The experiments on rapid conduction, which have been described, were conducted in the laboratory on shoots submerged in water. The same rapid conduction can also be observed in growing shoots provided they are sufficiently turgid. On an ordinary damp day, as is well known, conduction in the apical direction is often very slow, while basipetal conduction may be almost non-existent. A remarkable change occurs, however, under conditions of extreme humidity. The plants conduct stimulation through long distances in either apical or basipetal directions with velocities of over 100 cm. per minute, but the stimulus only affects the main pulvini and does not cause movements of the leaflets.

On one occasion, many experiments were carried out under such conditions. Heavy rain had fallen continuously for about three hours and light rain was falling at the time the experiments were performed. The weather for some days previously had been very wet and the ground was thoroughly saturated. The temperature was about 27° C.

The growing shoots were stimulated by burning the apex or a middle internode, or merely by nipping off the terminal bud between the finger and thumb. About 10 per cent. of the shoots failed to react, but the remainder showed rapid conduction. In 10 experiments the velocity varied from 1.1 to 2.8 cm. per sec. The mean velocity was 2.1 cm. per sec. over an average distance of 22 cm. The actual distance traversed by the stimulus in the basipetal direction was usually much greater, 30-40 cm., but owing to the fact that the plants were growing in a thick clump, it could not easily be measured.

After the main pulvini had reacted, the leaflets remained expanded, provided they did not knock against other leaves or branches as they dropped. If this occurred the leaflets closed, showing that they were sensitive to direct stimulation. When a petiole was cut or burnt, the main pulvinus reacted, but in most cases, transmission into the stem did not occur, although occasional positive results were obtained.

On the day on which these experiments were carried out, no examples of normal conduction in the stem could be observed, but on another damp day, on which the humidity was not quite so great, several instances occurred which indicated the overlapping of the two methods of conduction. The shoots were more or less horizontal, and were stimulated with the flame of a match in a middle internode. In one case, a leaf 9 cm. from the burn moved after 5.5 secs. The next leaf, 14 cm. from the burn, did not move until 5 mins. 15 secs. had elapsed. Another example showed the possibility of rapid conduction outstripping the normal type. The two leaves, 1 and 2, at either end of the stimulated internode reacted during the burning. Leaves 5 and 6 on the basal side moved together after about 9 secs., while the intermediate leaves, 3 and 4, reacted respectively after 3 mins. 10 secs. and 5 mins.

On the same occasion two other shoots showed one or other form of conduction exclusively. In one, the velocity was 15 cm. in 5 secs., in the other, 10 cm. in 2 mins. 20 secs. In both cases transport was in the apical direction.

RAPID CONDUCTION IN THE LEAF

It is an invariable rule that rapid conduction passing along the stem only affects the main pulvini and does not appear to enter the leaf. On the other hand, if a pinna of a leaf, which is submerged or floating on the surface of the water, is cut across, the main pulvinus reacts almost immediately and the leaflets also close. None of the other pulvini react, and therefore it may be assumed that the stimulus does not pass into the stem. Rapid conduction appears possible both in the leaf and in the stem, but its passage from the leaf to the stem, or from the stem to the leaf, seems usually to be blocked in the main pulvinus. For example, a pinna of each of two neighbouring leaves of a submerged shoot was cut across in turn. In each the main pulvinus moved almost immediately but the stimulus was not transmitted through the stem. Then the stem between the two leaves was squeezed with a pair of forceps. The stimulus passed through three internodes at a velocity of about 2 cm. per sec. A few exceptions occurred, as described before, in growing shoots when the petiole was burnt, but it is possible that transmission past the pulvinus was due to expansion of water in the tracheae under the action of heat, or to the co-operation of normal conduction.

The blocking effect of the pulvinus was also demonstrated by the following experiment. The petiole of a submerged leaf was held

between the finger and thumb to avoid movement, and then severed from the stem by cutting through the pulvinus with a pair of scissors. In the large majority of cases where this was done, the leaflets remained expanded, but when the petiole was again cut across just above the pulvinus, they closed almost at once. Although the cut through the pulvinus did not cause stimulation to pass out into the leaf, it was found, in most cases, to set up rapid conduction in the stem.

A blocking effect is also described by Snow (11) in the case of *M. Spegazzinii*. He found that in dry air the stimulus crossed over from one pinna to the other, but in damp conditions this did not occur, although the velocity of conduction was much greater.

It seems very probable that in the leaf, as in the stem, rapid conduction takes place by the successive contraction of turgid cells, the stimulant excreted by one cell causing the collapse of its neighbours and so on. This would provide the "relay mechanism" which Snow (11) considers necessary to explain the acceleration which occurs during the passage of a stimulus through the leaf of *M. Spegazzinii*. The fact that conduction in a turgid leaf is extraordinarily rapid, suggests that it is comparable to "high-speed" conduction in the stem, and is perhaps transmitted by the successive collapse of the tube cells in the phloem.

Snow, working both with *Mimosa pudica* (10) and *M. Spegazzinii* (11), has come to the conclusion that movement of water in the tracheae is insufficient to explain conduction of the stimulus in the leaf. This certainly seems to be the case in submerged leaves, although Ricca's experiments (8) on the movement of stains in the leaf, show that the tension hypothesis can explain a fairly high velocity of conduction under conditions of active transpiration.

The effect of turgidity on the rate of conduction is shown by the following experiments: Tests were made (A) on leaves of submerged shoots, (B) on leaves of growing shoots which were in the shade close to the ground, and (C) on leaves of growing shoots which were exposed to a strong sun. In each case a single pinna was cut across with a pair of scissors, and the time in seconds which elapsed before the main pulvinus reacted was noted. The times were as follows:

- (A). 1.5, 1.5, 1, 1, 0.5, 0.5, 1, 0.5, 1, 1.2, 1.5, 0.5, 0.5.
- (B). 1.5, 2, 1, 1, 2, 1.5, 2, 1.5, 2.5, 4.
- (C). 16, 3.2, 19.5, 1.5, 25, 3, 14, 12, 4, 24.

The average distance between the point of stimulation and the pulvinus was approximately 6 cm., and in the submerged leaves this distance was often traversed in as short a time as half a second.

In the shoots exposed to the sun, a rapid conduction occurred in 4 cases; in the others, the time taken for the stimulus to reach the pulvinus was at least three times as great, the difference in most cases being much more marked. There appears to be no doubt that these slower velocities were due to normal conduction by means of water currents in the tracheae.

Although Snow (11) has recognised that the velocity of conduction in the leaf is much greater when it is submerged or in a damp atmosphere, he apparently inclines to the view, advocated by Bose, that the conduction is a truly physiological process.

As an argument in favour of his own theory, Bose (2) quotes an experiment to show that the velocity of propagation in the petiole was increased, not by high turgidity, but by partial desiccation by means of glycerine. He regards this increase as comparable to what occurs in the animal nerve under similar conditions. It seems probable, however, that in this case he was dealing with "normal" conduction, and that the higher velocity was due to the greater tension in the water in the tracheae. The fact that in the "rapid" form of conduction, a close connection exists between high velocity and high turgidity, makes it much more probable that the conduction is not due to the propagation of nervous impulses, but to a mechanism which only comes into play when the cells are fully turgid.

The whole problem of the conduction in the leaf is, however, much more difficult than in the case of the stem, and more work will be required before it can be solved in a satisfactory manner. There seems to be no doubt that there are two distinct methods of conduction, as otherwise it would appear impossible to explain the very rapid conduction which takes place in highly turgid leaves.

The methods of conduction occurring in the stem and in the leaf appear to be of the same fundamental nature, although differences in anatomical structure may give rise to differences in velocity of conduction.

CONCLUSION

It appears to be certain that there are, in fact, at least two methods by which stimuli can be transported in *Mimosa*. One operates best when turgor is low and tension in the tracheae is great, and the other when the cells are in a condition of maximum turgidity.

Although both methods can operate at the one time in the same shoot, there is no gradual transition between the two. Rapid conduction finds its lower limit at a velocity which is not much less than

60 cm. per minute, whereas the highest rate found by Snow⁽¹⁰⁾ for normal conduction was 52 cm. per minute. This occurred under conditions of exceptionally high tension in a cut shoot. It is very probable that the cohesion theory of the ascent of sap would be quite adequate to explain a much higher velocity than this, provided conditions were suitable. It must be remembered, however, that the change from normal to rapid conduction does not take place when the former has reached a high rate, but rather when it has been reduced to a minimum.

Stated briefly, the essential difference between normal and rapid conduction is as follows: In normal conduction, the hormone which is liberated at the point where the stimulus is applied, is transported by the movements of the water current. In rapid conduction, it may be assumed that the hormone set free at the point of stimulation merely causes contraction of neighbouring cells, probably situated in the pith, and these in turn liberate a further quantity of the hormone, and so on. Thus a perfect relay mechanism would be provided, by which stimuli could travel equally well in either direction, quite apart from the movement of the water current.

By the choice of suitable conditions such as can be obtained, on the one hand by submerging shoots in water, and on the other, by subjecting them to very active transpiration, it is possible to study either form of conduction by itself. Between these two extremes, both forms of conduction may take place at the same time, and to some extent may co-operate with one another. In the case of shoots or leaves attached to the plant, or with their bases in water, it is no easy matter, at times, to decide which of the two methods of conduction is operating to the greater extent. The realisation that all cases of conduction need not be referred to a single hypothesis, should do much to explain the discrepancies in the conclusions of different writers.

The exact relationship of "high-speed" conduction to the other forms is not yet quite clear. Probably it is of the same nature as "rapid" conduction, and is effected by the almost explosive contraction of highly turgid cells, but differs in being propagated by the phloem instead of by the pith.

It is not proposed to discuss here the evidence brought forward by Bose⁽²⁾ in favour of the propagation of nervous impulses. It is quite obvious that many of his results can readily be explained in other ways. The evidence against the view that stimuli are transported in *Mimosa* by a nervous mechanism is so overwhelming, that

one is justified in neglecting this theory unless it is proved to be the only explanation of certain observed facts.

SUMMARY

Rapid conduction of stimuli can occur in shoots of *Mimosa pudica* which are submerged in water. The velocity usually varies from 100–200 cm. per minute, and stimulation is confined to the main pulvini and does not pass out into the leaves.

The complete removal of all tissues external to the wood, for a distance of as much as 6 cm., has no influence on the conduction.

Although a slight tension can exist in the water in the tracheae of a submerged shoot, this factor does not seem responsible for rapid conduction, which occurs independently of appreciable water movement.

The mechanism of rapid conduction appears to involve the successive collapse of highly turgid cells in the pith. As the cells contract they eject a stimulant which causes the contraction of neighbouring cells, and so the process goes on.

Rapid conduction can occur in growing shoots provided they are sufficiently turgid. It can also occur in leaves, but the passage of the stimulus by this method from leaf to stem, or from stem to leaf, is usually blocked at the main pulvinus.

There are at least two distinct methods by which stimuli are conducted in *Mimosa*. The relationship of the different forms of conduction to one another is discussed.

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THE HISTOLOGY OF THE COLEOPTILE IN
RELATION TO ITS PHOTOTROPIC RESPONSE

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(With 8 figures in the text)

I. INTRODUCTION

SINCE the publication of the *Power of Movement in Plants*, the coleoptile of the Gramineae has been the classic example of an organ which carries out a directional movement at the unilluminated base when the apex is exposed to one-sided lighting. This movement has been explained on the basis of the existence of systems of stimulus, excitation and response. The stimulus is received at the apex, it is then carried down to the base in some way, and here the responsive machinery is set going. The mechanism of response is undoubtedly the unequal growth of the cells on either side of the coleoptile, but the mechanism of reception of the stimulus is still quite unknown.

New light seemed to be thrown on the subject by an experiment first performed by Boysen-Jensen and since frequently repeated, which showed that the curvature towards the light could still follow even if the apex was cut off and was replaced by the help of gelatine before being subjected to unilateral light. This type of experiment suggested that the mechanism of transmission was to be found in substances capable of diffusion through gelatine which were released at the apex, and which travelled to the base before the response took place. These hypothetical substances were frequently classed as "hormones" and experiments on the lines of those mentioned above represent the main experimental grounds for assigning a rôle to hormones as a co-ordinating influence in the life and growth of the plants. This machinery of reception, transmission and response has been applied to the growth movement of the coleoptile without any direct investigation of the nature of the tissues of this organ. No data have been given as to the cytology of the apical cells which are supposed to be active in the secretion of the hormones. Also, when the apex is cut off, the tip of the stump is again sensitive to light within 14 hours, and it is therefore assumed that a new apical system

has been regenerated capable of secreting hormones, but no microscopical examination of the tissue has been made to corroborate this statement. The channels of downward transmission of these substances are unknown, but Fitting has supplied experimental grounds for the conclusion that the veins are not the only possible path. No mention has been made of the difficulty created by the constant upward movement of sap in the growing coleoptile which results in guttation from the apex when the roots are freely supplied with moisture and the shoot is in moist air. The actual mechanism of tropic curvature is known, but no detailed examination of the tissues has been made such as would permit an analysis of the unequal growth extension responsible for the curvature under different conditions. In view of the great theoretical importance of the interpretation given to the tropic responses of the coleoptile, these are very important lacunae in our information, and the following account is the result of an attempt to fill up these gaps in our knowledge of the coleoptile.

2. THE DEVELOPMENT OF THE COLEOPTILE

The coleoptile of various members of the Gramineae has been studied, but the following account is based mainly upon *Zea mays*, although practically every point has been verified in *Avena*, of which a pure line was available for study through the courtesy of Sir R. H. Biffen.

In the embryo, the coleoptile forms a complete cylinder, closed by a blunt cone at the apex and this encloses the rolled first foliage leaf within it. The whole organ is composed of meristematic cells at this stage, and the future vascular bundles are visible as two procambial strands, the cells of which are very small in transverse section (Fig. 1). Almost as soon as water is absorbed by the embryo on germination, this meristematic condition disappears. If the grains are soaked in water for a few hours and the coleoptile is removed and sections are cut, it will be found that all regions of the coleoptile except the vascular strands are vacuolating. No cell divisions in the tissues of the coleoptile have been seen, but it is possible that such divisions have been missed in the procambial strands, many elements of which remain densely packed with protoplasm for some considerable time. Serial microtomed sections of the coleoptile were made at different stages in its development, as well as hand sections of fresh material. In daylight, at normal temperatures, the coleoptile reaches its full extension in length in five days, but at low temperatures (Vögt⁽¹²⁾), or when grown in continuous

darkness, it continues to extend for some days longer. Its development has been followed when grown under various light conditions, and in the following account the normal daylight-grown structure is described with occasional reference to differences noted when grown under other conditions.

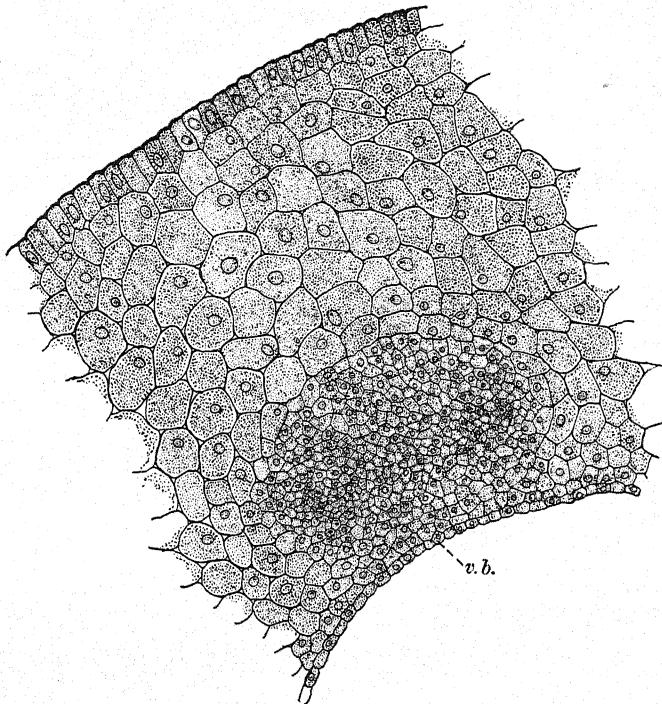


Fig. 1. T.S. of part of coleoptile of *Zea mays* in meristematic condition.
v.b. = vascular bundle.

In transverse section, the maize coleoptile is oval in shape, the thickest part of the cylinder being in the greatest diameter of the oval (Fig. 2).

Two vascular bundles run up parallel with each other in the positions indicated in the same figure. The course of the bundles is parallel up the length of the coleoptile but, at the apex, the bundles converge somewhat towards the "back" of the coleoptile (i.e. the side away from the grain and from the split formed subsequently by the emergence of the first leaf). This convergence at the tip is especially noticeable in the case of *Avena* and *Hordeum*. Each

bundle ends in an irregular group of small tracheids which run out towards the surface, and lie just below a group of stomata. The two bundles are not given off at the same level at the junction of the mesocotyl and coleoptile; the first one to be given off reaches a slightly lower level than the parallel bundle on the opposite side of the coleoptile. Stomata are present throughout the length of the coleoptile, but they are confined to the epidermis in the region lying above the bundles. This region narrows down considerably over the bundle endings above which a few stomata are grouped (Fig. 3).

During the earliest stages of the development of the embryo, the growth of the first leaf keeps pace with that of the coleoptile.

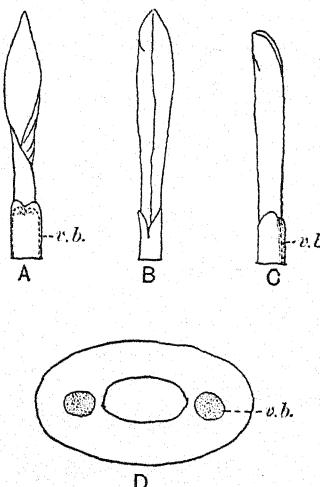


Fig. 2. A, B, C, back, front and side views of coleoptile; D, transverse section of very young coleoptile. *v.b.* = vascular bundle.

Later, however, the leaf continues to grow when the coleoptile has ceased to elongate with the result that the latter is then split just below its apex on the side towards the grain, and it then forms a sheath round the base of the developing first leaf.

The coleoptile is practically colourless at first, but in about 10 days' time, when the first leaf is well grown—it becomes greener owing to the appearance of chloroplasts in the outer layers of cells below the epidermis and especially in the region of the vascular bundles. (Fig. 4.)

Although the growth in length of the coleoptile stops in five days, the differentiation of the coleoptile continues and, after growth has

ceased the vascular bundles become much more prominent until finally the coleoptile looks like a transparent membrane supported by two very dark brown vascular bundles. Sections cut at various levels show that at this stage all the chloroplasts have degenerated

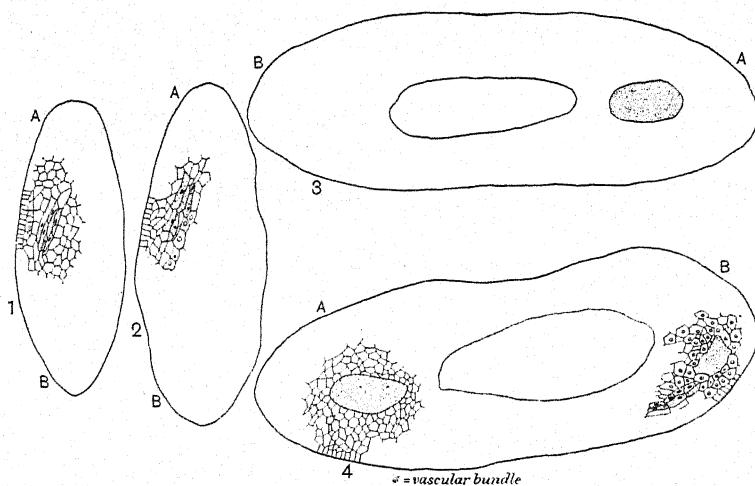


Fig. 3. A and B indicate corresponding sides of coleoptile in series.
 1. 4th section of series from apex. 3. 14th section of series from apex.
 2. 7th " " " 4. 32nd " " "

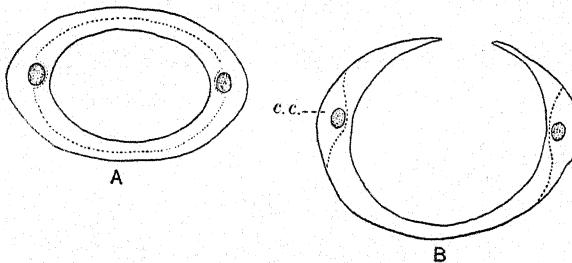


Fig. 4. A, diagram of transverse section near base of coleoptile; B, diagram of transverse section near apex of coleoptile. c.c. = chloroplast-containing cells.

except, near the base, where normal chloroplasts are to be seen round the bundle. In the latest stage of all, the cells of the coleoptile begin to shrivel from the apex downwards and the cells collapse, except those immediately surrounding the vascular bundles and the inner and outer epidermis.

3. DEVELOPMENT OF VASCULAR SYSTEM

Various developmental stages are passed through by the vascular bundles during the 35 days they take to complete their differentiation. In the embryonic condition, they consist of minute uniform cells with dense cell contents. The first vascular elements to be differentiated are those of the protoxylem vessels towards the inside (i.e. morphologically upper side) of the bundle. Later, and separated from the protoxylem by a row or two of parenchyma, the metaxylem elements appear and form a curved line round the inner margin of the bundle. This stage appears to last until the cells of the coleoptile have nearly finished elongating. The central and outer cells of the bundle then become vacuolated forming thin-walled cells (which later become thickened) and two groups of phloem become distinguishable owing to the dense contents of their cells and their differentiation into sieve tubes and companion cells.

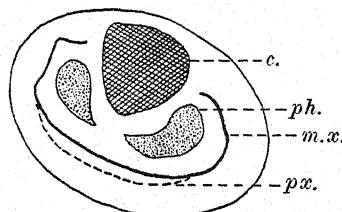


Fig. 5. Transverse section of vascular bundle of Maize. *px.* = protoxylem; *m.x.* = metaxylem; *ph.* = phloem; *c.* = collenchyma.

When the coleoptile commences to shrivel, all the cells of the vascular bundles, except the xylem, have been thickened by the deposition of cellulose evenly over the surface of the walls. This fact can be demonstrated by means of chloriodide of zinc or iodine followed by sulphuric acid, the cell walls turning the characteristic purple-blue given by cellulose. The only elements giving lignin reactions are the metaxylem elements which stain faintly red with phloroglucin and hydrochloric acid. The differentiation of the xylem proceeds from the base to the apex, but the process is evidently quite rapid since any difference in the amount of xylem present in the upper and lower parts of the coleoptile is only noticeable in young coleoptiles. When compared with the rapid differentiation of the other tissues of the coleoptile, the differentiation of the vascular bundle is comparatively slow. No phloem is distinguishable until after the coleoptile has completed its growth in length. The last

stage in its development is the gradual thickening of the walls of the cells around and between the two phloem groups. It is only in the last stage that differences can be noted in the bundles of coleoptiles grown in light and those grown in darkness. In daylight cellulose is deposited uniformly over the walls of these cells and not very thickly, but in continuous artificial light (100 watt Osram lamp at a distance of about half a metre) the cellulose is deposited more heavily, especially at the angles of the cells, so that the vascular elements are embedded in a tissue resembling collenchyma, which was especially strongly developed around the phloem. A similar collenchymatous tissue developed in coleoptiles which, after ten days' growth in darkness, were grown for eleven days in ordinary daylight.

4. THE PARENCHYMA OF THE COLEOPTILE

The history of the development of the parenchyma of the coleoptile is mainly a story of cell vacuolation and extension, but there are certain points of interest. Vacuolation commences at the apex, but the cells in this region never extend much in length. Their walls are apparently too set at the time that vacuolation occurs to admit of elongation and this cone of differentiated, almost spherical, cells seems to block the further apical differentiation of the bundles, which are thus diverted obliquely towards the back of the coleoptile. These cells are singularly unlike the type of cell which is usually regarded as active in secretion. When vacuolation first begins the cytoplasm contains starch grains, this is true of the ground tissue throughout the length of the coleoptile. These grains are first of all somewhat difficult to find with iodine reagents, unless the sections are first treated with eau de javelle. In the fixed material, they stain readily with cotton red or gentian violet and are present in the cells prior to vacuolation. These grains then disappear slowly in coleoptiles grown in the dark, but much more rapidly after exposure to light (Zollikofer (13)). In either case starch disappears from the apex first, and then continues basipetally. After the starch has disappeared, no further changes can be seen in any of the apical cells until they die; the cells in this region are the first to collapse as the coleoptile shrivels from apex to the base. It is usually assumed that the apex consists of cells active in metabolism. Söding has further assumed that when the apex is removed by a transverse cut as in so many recent tropic experiments, a new apical tissue is regenerated at the apex having a similar active metabolism. This original active metabolic tissue is, however, a myth and examination

of the stump after removal of the apex shows, as might be expected in a tissue of this type, that absolutely no regeneration of cellular tissue takes place. After standing for 48 hours in damp air no new cells had formed, nor indeed in other stumps after 21 days. As is shown in Fig. 6 the cells at the cut surface contract somewhat, the cut surface dries back till an undamaged cell is reached and upon this a deposit of fatty and other substances occurs which gradually blocks the wounded surface.

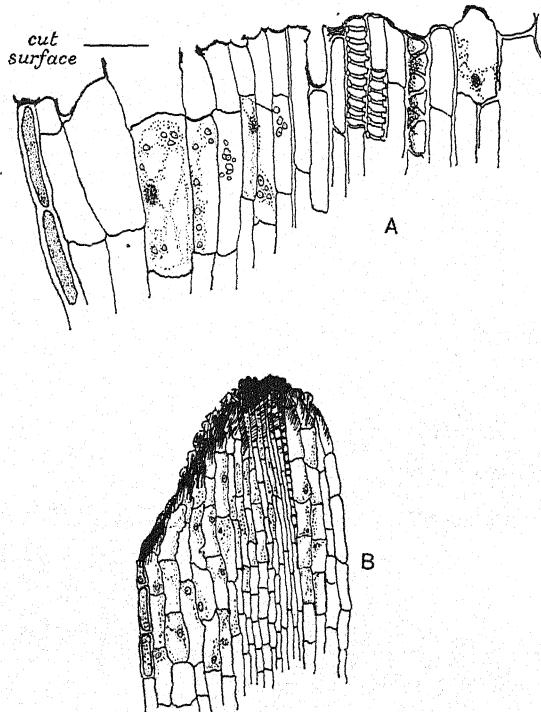


Fig. 6. A, Longitudinal section of part of stump of Maize coleoptile after 3 days; B, ditto after 21 days.

Below the apical cone of differentiated cells, the parenchyma cells with extensible walls are found and it is in this region that the active elongation of the coleoptile occurs. The process of vacuolation spreads to the base of the coleoptile with very great rapidity, so that it is very difficult to obtain any intermediate stages between the slight vacuolation of cells at the apex and vacuolations of cells throughout the whole length of the coleoptile. The process of elonga-

gation is associated with the disappearance of starch and the entry of water—processes which are facilitated by exposure to light. It follows, therefore, that the tropic curvatures of the coleoptile also must be due to a large extent to these processes, and on these grounds they deserve some examination in detail—if only to correlate cell extension with coleoptile extension.

To this end, the daily extension of a number of coleoptiles was measured and subsequently the same coleoptiles were cleared by treatment with alcoholic hydrochloric acid. The coleoptile was then mounted whole, and a series of cells—usually epidermal cells—was taken from the apex to the base of the coleoptile. These could be followed under the microscope with an eye-piece micrometer, and the length of each cell recorded.

There are already in the literature ((10) and (12)) very careful studies of the growth of the coleoptile under constant temperature conditions and under various light exposures. The present data confirm the earlier observations and permit some interpretation of them in the light of this detailed microscopic examination.

Coleoptiles were grown sometimes in daylight in the greenhouse without further temperature control and in other cases in a thermostat at nearly constant temperatures in darkness or in intermittent or continuous artificial illumination.

Vögt's studies led him to the conclusion that light shortened the growth period of the coleoptile. The greater the intensity of the light, the smaller the maximum growth rate and the sooner growth ceased. Also, with increasing light exposures, whether of time or intensity, the ultimate length reached by the coleoptile became less to an extent roughly proportional to the quantity of light employed. At higher temperatures the velocity of growth was greater, but the duration of growth definitely smaller. At a temperature of 7.5° C., the coleoptile (of *Avena*) might grow for 30 days instead of the 5 days for which growth continues at 20° C. The maximum final length was obtained at 12.8° C., and above and below this temperature the final length began to diminish with brief light exposures. If the light was sufficiently intense, an original retardation of growth was followed by a marked acceleration. This effect was still obtained, even if the coleoptile was subjected to weak illumination after, or before, the brief intenser light exposure.

Vögt's general results as to the effect of light upon the rate of growth of the coleoptile, the duration of growth, and upon the ultimate length of the coleoptile are supported by the following data

from Maize coleoptiles grown at the same temperature under various light conditions. In complete darkness, however, the duration of growth of the coleoptiles of *Zea mays* was 8 days as compared with 5 days at the same temperature in the case of *Avena* (Vögt).

I. Continuous Dark. Temp. 21-23° C.

Length (cm.)

1st day	0.5	0.3	0.5	0.5
2nd "	0.9	1.0	1.1	0.8
3rd "	1.4	2.5	2.4	1.3
4th "	2.5	4.1	3.8	2.8
5th "	3.6	5.3	4.6	3.0
6th "	4.8	5.7	5.1	3.6
7th "	5.2	5.9	5.2	4.2
8th "	5.2	5.9	5.2	4.2

II. Continuous Light. 60 watt lamp.

1st day	0.5	0.3	0.3	0.4
2nd "	1.0	0.8	0.9	1.0
3rd "	2.5	1.9	2.5	2.5
4th "	3.4	3.1	3.1	3.3
5th "	3.6	3.6	3.3	3.6
6th "	3.6	3.6	3.3	3.6

III. 6 hours light per day. 60 watt lamp.

1st day	0.3	0.3	0.3	0.3
2nd "	1.0	0.8	0.8	0.9
3rd "	2.0	2.3	2.4	2.3
4th "	3.6	3.9	3.0	3.8
5th "	4.3	4.3	4.0	4.3
6th "	4.3	4.3	4.0	4.3

IV. Continuous Light. 100 watt lamp.

1st day	0.4	0.5	0.4	0.6
2nd "	1.2	1.4	1.2	1.4
3rd "	2.2	2.1	1.9	2.2
4th "	2.5	2.2	2.3	2.6
5th "	2.5	2.2	2.3	2.6

V. 6 hours light per day. 100 watt lamp.

1st day	0.3	0.5	0.4	0.4
2nd "	0.6	1.4	0.8	0.9
3rd "	1.9	2.7	1.7	2.3
4th "	3.0	3.8	2.6	4.0
5th "	3.7	4.0	2.9	4.0
6th "	3.7	4.0	2.9	4.0

It will be seen that the growth is more rapid under continuous or intermittent lighting, but continues much longer in the dark so that ultimately the longest coleoptile is that grown in the dark.

In Fig. 8, the relative lengths of a series of cells from the coleoptiles are plotted, the abscissae representing the number of the cell proceeding in order from the base, the ordinates giving its length in terms of the scale of the micrometer eye-piece.

The cells at the apex are not elongated, and consequently their measurement as a continuous row is difficult. It was noticed that in continuous light the cells at the apex were smaller, and had thicker walls than those grown in darkness, and a smaller proportion of the cells had succeeded in elongating. Probably about the same number of cells elongated in intermittent light (6 hours) as in darkness, but

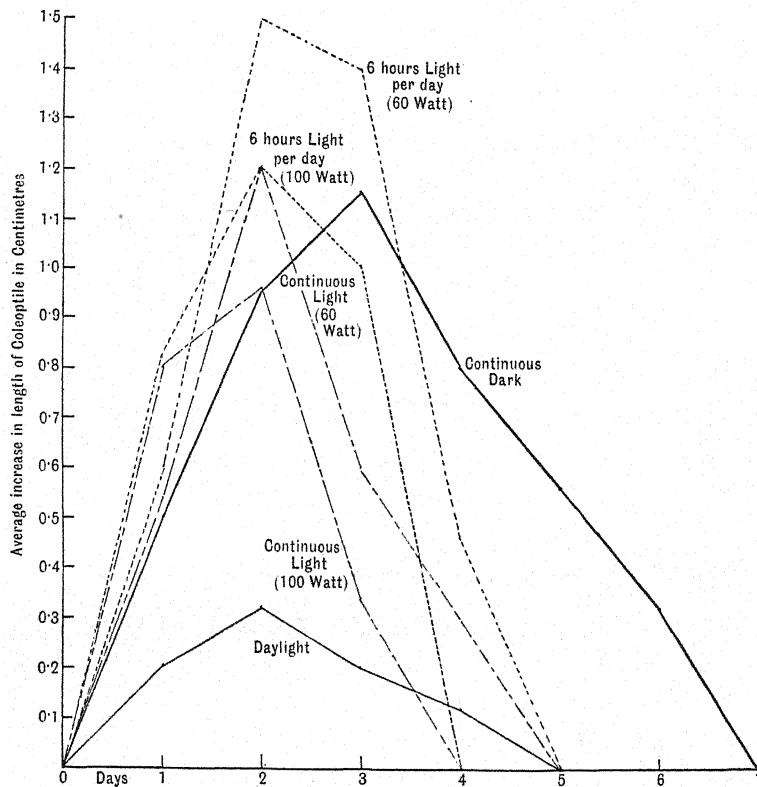


Fig. 7. Graph showing average increase per day under different light conditions.

the greater length of the coleoptile in darkness was due to the greater elongation, on the average, of the cells in the dark.

It would appear then that in the light a process is at work from the apex downwards which prevents the continued elongation of the cells. In the light the cells probably commence to elongate more rapidly (i.e. the water enters the cell earlier) and, therefore, in the light, more cells are elongating at the same time, and the process of elongation begins a few cells lower down from the apex in light than

in darkness. In the dark the process of elongation continues for a longer period in an individual cell.

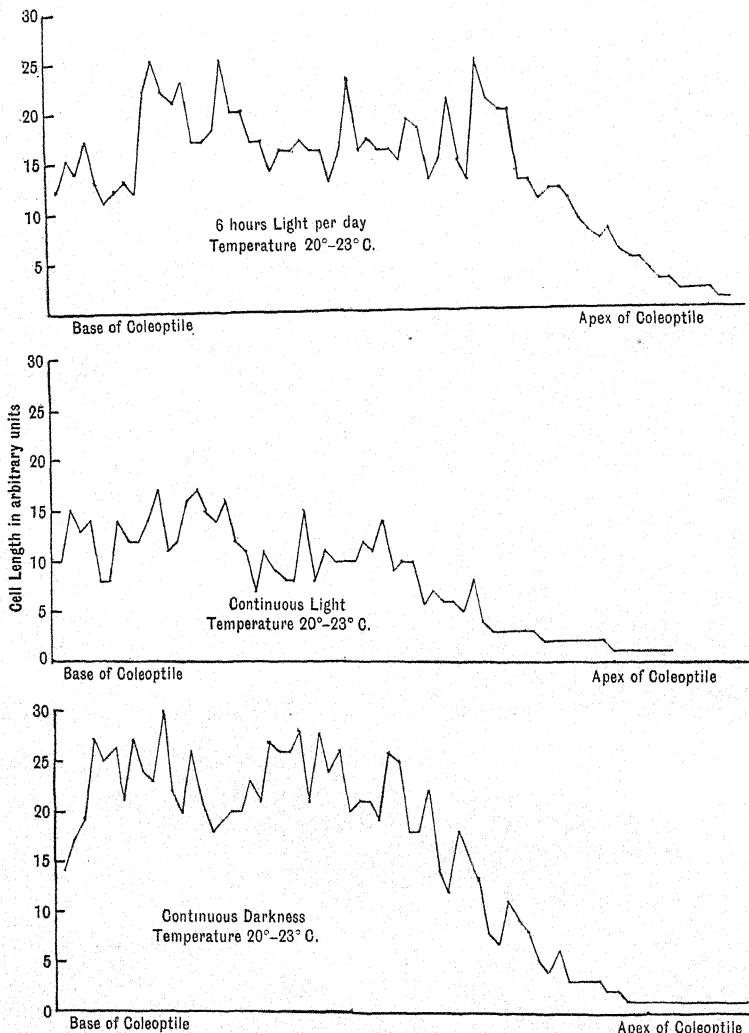


Fig. 8. Graph showing relative length of cells from base to apex of coleoptile under different light conditions.

These results suggest that light facilitates elongation and renders it more rapid from the apex downwards by increasing tissue permeability and, therefore, the access of water to the cells. It diminishes

the final length of the coleoptile by decreasing the time over which elongation can go on, probably because it leads to chemical changes in the wall which increase resistance to stretching, these changes proceeding first at the apex which is most exposed and then from the apex downwards. Temperature changes probably act similarly, in that high temperatures accelerate the rate of wall change in the direction of higher resistance to stretching.

These results then seem to give a fairly complete explanation of Vögt's earlier observations. On sudden exposure to relatively intense illumination, there is a temporary fall in sap supply to the already elongating cells due to increased apical guttation, and a wider spread of the sap in the tissues owing to increased tissue permeability. As more sap arrives from the root system this is followed by a more rapid elongation because a wider zone of cells is now elongating, but the final length of the coleoptile is less because the time over which elongation can go on is lessened owing to the increased wall resistance.

5. DISCUSSION

In the light of these facts as to the development and histology of the coleoptile, it is difficult to see how the classic view of reception, transmission and response can be maintained in the case of the coleoptile.

The reception of the stimulus by the apex from the standpoint of this theory has always been a subject of controversy. Recently Lundegårdh(6) has been the most vigorous supporter of the theory that the angle of incidence of the light is the determining factor in direction, or rather the angle of penetration, of the cell. Lundegårdh considers that the path of the refracted light ray entering the cell is the significant factor which determines the direction of responsive curvature. This is, however, a singularly difficult direction to determine—as both Lundegårdh's and Von Guttenberg's(5) experiments indicate—when the light is being received on the sharply sloping apex of the coleoptile. Von Guttenberg finds that rays falling on the apex from a level a little above it, are much more effective than rays striking on the apex equally from the side, but from a point below the apex. These experiments and others in which one side only of the coleoptile is lit vertically from above lead to the conclusion that curvature is determined by the unequal intensity of the illumination on the apex and not by the direction of the incident radiation, a conclusion with which von Guttenberg's experi-

ments agree. In no case however is any attempt made to indicate the nature of the light effect upon cells at the apex of the coleoptile. Lundegårdh treats the apex as if it were a perfectly radial organ and no observer seems to see any possible significance in the presence of two hydathode areas just below the apex on one of the broader flanks. Fig. 3 shows how the veins running up the narrow flanks bend outwards and sideways and end in a group of tracheids lying just below the surface on one of the broad flanks. The flow of sap outwards through the stomata covering this hydathode depends upon the pressure of sap on the vascular system and the tissue permeability of the thin screen of living cells blocking the passage of the sap to the outside. This tissue permeability has been shown on many occasions now⁽⁹⁾ to be very sensitive to light exposure in organs grown originally in the dark. Such increased tissue permeability on exposure to lateral light would readily lead to asymmetric release of sap, especially if the light fell upon one of the narrow flanks, and many observers have placed on record the fact that the response of the coleoptile to lateral illumination of the apex is more regular and reliable if the narrow flank is turned towards the source of illumination.

According to the classic theory, whatever the nature of the light reception by the cells, it should lead to the release of special growth-controlling substances from the cell. From the standpoint of some investigators (e.g. Brauner) these apical cells must always be releasing these substances and their rate of passage down the flank is influenced by illumination and Paal⁽⁷⁾ suggests that the light effect may lead to a partial destruction of the substance thus formed. The details as to the nature of the apical tissue given previously do not suggest in the least a tissue active in secretory metabolism. The cells are the first to vacuolate and the first to die.

Again, the explanation given by Söding of his experiments receives absolutely no support in the light of these facts. Söding assumes that the secretory apical tissue has been regenerated in a coleoptile stump since its sensitiveness to lateral apical illumination returns after a short period of time. But actually no new cells are formed at all, this tissue evidently being completely incapable of regeneration. All that has happened has been a gradual blocking of the cut surfaces and probably when the stump is unequally illuminated the tissue permeability is asymmetrically affected and sap leakage occurs more from one side of the blocking stump than from the other. Söding's experiments in the light of their histology become

strong experimental support for the view that the apical reception of the tropic stimulus is independent of any mechanism involving special secretory cells. The possible paths of transmission of the stimulus downwards have also been a difficulty. Little new light is thrown upon this part of the subject by the anatomical data provided, but it is pointed out that the usual assumption that the vein away from the light is active has to meet the difficulty that the substances are diffusing against a constant upward flow of sap to, and through, a hydathode. A downward passage through the phloem may be suggested. It is therefore relevant to emphasise the fact that the differentiation of the phloem is not complete until the full extension of the coleoptile has taken place and growth curvatures are no longer possible.

The mechanism of response is clearly unequal cell extension, which is affected by light in two ways, (1) by the increased resistance to stretching induced by the action of light upon the walls—an effect which is only produced upon walls exposed to the light, and (2) by the increased rapidity of entry of water and of the movement of sap generally, which is the result of the increased tissue permeability that follows exposure to light. This effect may be exerted either directly upon the illuminated tissue or indirectly through its effect in reducing the sap pressure in the vascular system as the result of the greater leakage at the apex. There seems no necessity to assume that any hypothetical substances are diffusing from the apex, and until such hormones are experimentally demonstrated they may quite well be dispensed with in theories of tropic response.

6. SUMMARY

1. The histology and development of the coleoptile have been passed in review in order to see what light the details of structure and development throw upon the machinery of phototropic response in that organ.

2. The data obtained, especially as to the nature of the cells at the apex of the coleoptile and as to the absence of apical regeneration in the decapitated stump, are in complete disagreement with the classical view as to the rôle of the apex in receiving and transmitting a tropic stimulus.

3. The data given are in harmony with a simpler explanation of the tropic response recently put forward in which light acts by increasing tissue permeability and by hastening the change in the chemical nature of the cell walls which diminishes their extensibility.

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THE RELATION BETWEEN RESPIRATION AND
WATER CONTENT IN HIGHER FUNGI

WITH A NOTE ON THE EFFECT OF LIGHT ON RESPIRATION

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(With 4 figures in the text)

INTRODUCTION

THE relationship which exists between all physiological processes and water is a fundamental one, and the importance of water in plants cannot be emphasised too strongly. It is produced during respiration, and, according to modern theories, is necessary to initiate this process. Therefore the question of the connection between respiration and water content is one of some importance. Work has already been done by physiologists, in this connection, using some groups of plants, but the relationship in fungi does not appear to have been investigated.

It has been observed that thoroughly dried seeds, mosses, and lichens do not respire, although respiration begins when but little water is present, and rapidly increases as more is absorbed. On the other hand, the injection of stomata or intercellular spaces with water renders gaseous interchanges more difficult, and thus diminishes the respiratory activity. Kreusler^(7, 8) found that leaves respire most rapidly when in the normal turgid condition. Aubert⁽¹⁾ obtained similar results with members of the Crassulaceae, and Jumelle⁽⁶⁾ with lichens. Recently, Mayer and Plantefol⁽⁹⁾ performed a series of experiments on *Hyphnum triquetrum*, and found that the rate of respiration depends on the water content, an optimum water content lying between 46 per cent. and 60 per cent. of the fresh weight.

Ilijin⁽⁵⁾ states that although there is a great decrease in respiration as seeds ripen, this is not due solely to the decrease in water content, but partly to changes in the plasma. Experimenting with the leaves of a number of genera of plants (*Triticum*, *Salsola*, *Rumex*, *Bidens*, *Centaurea*, *Statice*, *Trifolium*, and *Ranunculus*), he found two types: (1) leaves, usually belonging to xerophytes, showing only a decrease in respiration on losing water; and (2) leaves belonging generally

to plants from moist habitats, showing, on losing water, an increase in respiration to a maximum, and then a decrease. He suggests that there may possibly be a maximum even in the first group, but if so it is not observable since it occurs at a high water content.

In connection with this, it is interesting to note that Hée⁽⁴⁾ (experimenting with entire plants of *Brassica napus*, *Allium porrum*, *Lupinus albus*, and *Vicia faba*, of very different weights, but otherwise under as nearly identical conditions as possible) found no relation between the carbon dioxide of respiration and either the fresh or dry weights of the plants.

No investigations of a similar nature for fungi are recorded, although Bonnier and Mangin⁽²⁾ found that the respiratory rate of the sporophores of some Hymenomycetes increases with the humidity of the air, being greatest when the atmosphere is saturated. Pieschel⁽¹⁰⁾ states that the transpiration of fungus sporophores, at different temperatures, is approximately proportional to the saturation deficit of the air, and that different species hold water with different degrees of tenacity; placing most fungi in water causes a complete elimination of transpiration loss, but this is not the case with *Amanita* and *Lactarius*.

APPARATUS, ETC.

The apparatus used is one whereby the carbon dioxide is estimated by absorption in baryta, and the oxygen by observation of the change in pressure which occurs in the closed respiratory chamber during the course of the experiment. The fungi are placed in the glass chamber *A* (see Fig. 1), which again is placed in the water-bath *B*. The chamber is provided with a thermometer *T*, and two tubes *C* and *D*, each tube being connected to a two-way tap. By means of these taps the chamber can be placed in communication with either of the tubes *G* and *H*, and with either *M* or *N*, or else cut off from all external communication. The tube *G* leads to two Wolff's bottles, *K* and *J*, *K* containing a strong solution of caustic potash, and *J* one of baryta; thus air freed from CO_2 can be introduced into the apparatus. *H* connects the respiratory chamber with a water manometer *L*. *M* leads to an extraction apparatus, by means of which a known volume of air may be drawn from the chamber; this apparatus is used for determining the volume of air surrounding the fungi. Finally, the tube *N* is connected, at the close of the experiment, with the Pettenkofer tube *P*, containing the standardised baryta solution. From here the air is drawn, by means of a water pump, through the

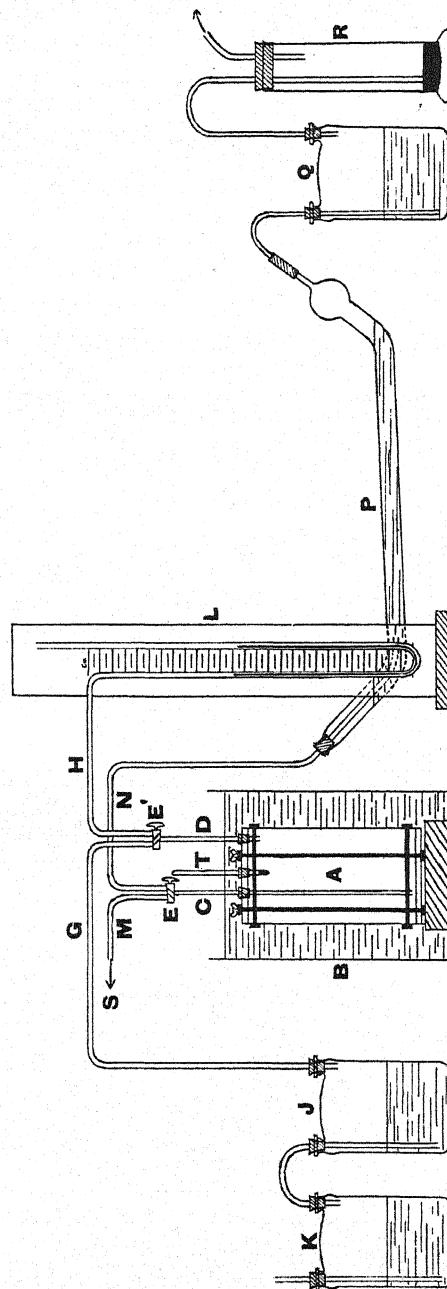


Fig. 1. Diagram of apparatus used (for description see text).

Wolff's bottle *Q*, which contains baryta water to ensure that all the CO_2 of respiration has been absorbed by its passage through *P*. Hence it passes through the vessel *R*, containing mercury, the resistance of which renders the flow of air through the apparatus as steady as possible. When washing the chamber free of CO_2 in this manner, the course of the air through the apparatus is *K*, *J*, *G*, *A*, *N*, *P*, *Q* and *R*.

The water content of the fungi was determined by drying in an electric oven at 98°C . for several hours, according to individual requirements, finishing off at 102°C . for half an hour, or until the weight—on cooling in a desiccator—remained constant. In some experiments, the water content of the same sporophore was required on three or more successive days. In this case, the amount given for the last day only is correct, since the dry weight can only be determined once. As this must change to some extent during the period, the water content of the earlier determinations (obtained from the moist weight on any particular day and the dry weight at the end of the period) will not be strictly accurate.

EXPERIMENTAL RESULTS

At the outset, it may be stated that evidence has been obtained to show that a general relationship can be traced between the rate of respiration of fungus sporophores and their water content. Sporophores which have a low water content have also a low rate of respiration; and conversely, those with a high water content have also a high rate of respiration. There is evidence, at least in some species, of an "optimum" water content. The amount of water present in the tissues has apparently no effect on the respiratory coefficient, where this has been observed. The results obtained are detailed below.

(i) *Respiration during progressive decrease or increase of water content.*

Experiments were performed on the sporophores of three fungi, the same sporophores being tested at varying water contents. As such observations must of necessity extend over a few days, the species chosen were long lived, and, in two cases at least, xerophilous (i.e. fungi which, after thorough desiccation, can be again moistened out and continue to shed spores). In two cases (*Pleurotus ostreatus* and *Polyporus adustus*) the experiments were started at a high water content, and were performed on successive days, the fungi being

exposed in the meantime to the air, so that gradual desiccation took place. In the third case (*Stereum hirsutum*) the sporophores were gathered and exposed to the air of the laboratory for three days before the series of experiments was begun; after each experiment, they were exposed for a night to a moist atmosphere, this procedure being repeated until they could not be induced to take up more water. As these three species are very persistent, the rate of respiration due to ageing would fall off only to a small extent during the few days the observations were carried over. To make sure of this point, a sporophore of *Pleurotus ostreatus* was kept in a moist condition for four days, and the rate of respiration tested at the beginning and end of this time; this control showed that the rate of respiration fell off by less than 20 per cent. in this time. The point was also examined in the case of *Stereum hirsutum*; after the sporophores had been completely saturated with water, they were again exposed to the air for a night, and tested the following morning. The results showed that the curve obtained could be taken as an approximation to the true respiration-water content curve, apart from the effect of ageing.

The results are shown in the graphs (Figs. 2 and 3).

(a) *Pleurotus ostreatus*. The first set of experiments was performed on sporophores in their prime condition, the series being started at the water content they possessed at the time of gathering. The respiration-water content curve shows a steep gradient, which becomes less steep as the water content decreases. That is, the rate of respiration, as measured by the CO_2 output, decreases at a less rate per unit of water content decrease, the less the amount of water present in the tissues.

The second series of experiments was performed on specimens which had previously been exposed to very wet conditions, so that the initial water content was extremely high. The curve shows the same kind of change in gradient between 730 per cent. and 120 per cent. water content, but above 730 per cent. there appears to be a definite "optimum" for the rate of respiration (about 815 per cent.).

(These two curves show the actual amounts of CO_2 given off by the fungi in one hour, and not the amounts produced per gram dry weight, e.g. the difference in the initial amounts of CO_2 is not significant.)

(b) *Polyporus adustus*. The fungi were gathered and exposed for a day to a saturated atmosphere, until they would absorb no more water. There is no indication of the "optimum" water content

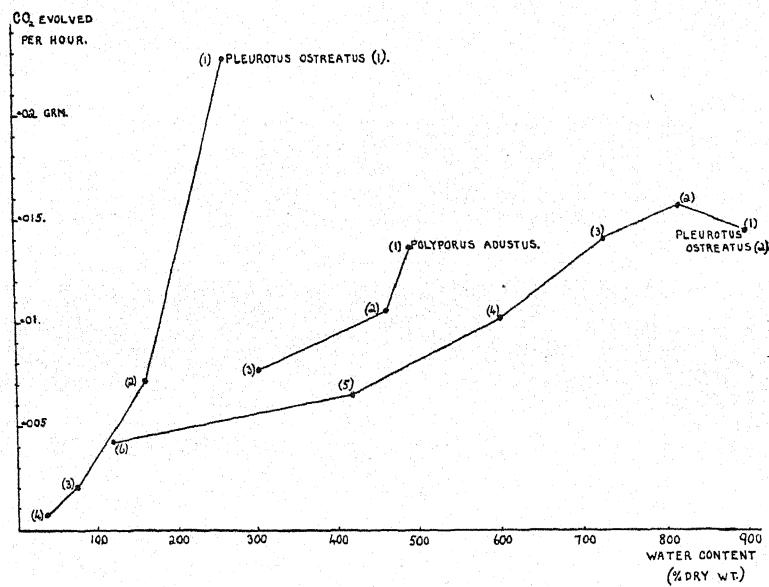


FIG II.

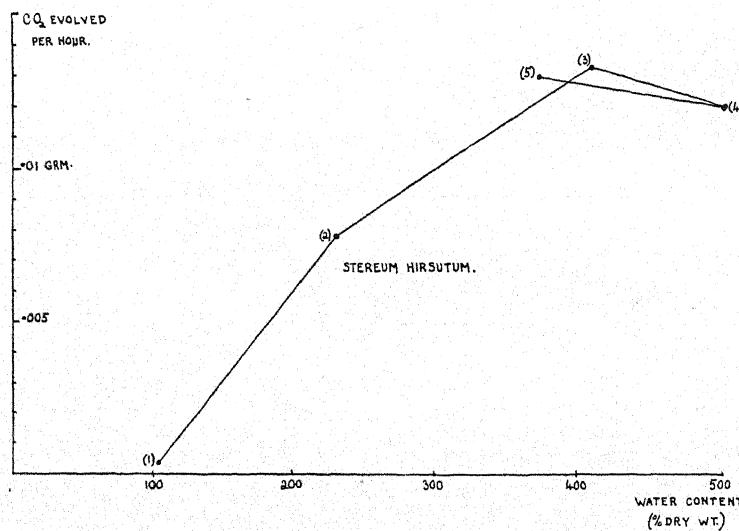


FIG III.

Fig. 2. Relation between rate of respiration and water content, during progressive decrease of water content, in *Pleurotus ostreatus* and *Polyporus adustus*.

Fig. 3. Relation between rate of respiration and water content, during progressive increase of water content, in *Stereum hirsutum*.

shown in the case of *Pleurotus*; it is possible that the tissues of this fungus will not allow the water content to reach the "optimum" limit. The curve is again concave to the rate-of-respiration co-ordinate.

(c) *Stereum hirsutum*. In this species there is again, apparently, an "optimum" water content as regards the rate of respiration, and this value again lies near to the limit of the amount of water which the fungus will absorb. The curve obtained, below the "optimum," is convex to the rate-of-respiration co-ordinate, but this form may be more apparent than real; possibly if a larger number of observations were taken, the curve would fall into line with those obtained for *Pleurotus* and *Polyporus*.

(2) *Relation between respiration and "normal" water content.*

Numerous experiments have been performed on freshly gathered sporophores of various species, and their rates of respiration and water contents observed. Different crops of each species were tested, and the results obtained for any one species were sufficiently constant to admit of a direct comparison of one species with another. Only in the case of one (*Polyporus adustus*) were the results obtained from different crops too variable to allow any comparison—probably on account of the different conditions under which these sporophores had previously grown. The experiments were performed on fresh, healthy sporophores, mature, but not decaying; and all at comparable temperatures (about 17° C.). The following table gives the results obtained—the amount of carbon dioxide evolved is expressed in milligrams per grm. dry weight of fungus material per hour, and the water content as percentage of the dry weight:

TABLE I

Species	CO ₂ evolved (mg.)	Water content* (%)
(1) <i>Coprinus micaceus</i>	8.9	1800
(2) <i>Marasmius conigenus</i>	6.7	760
(3) <i>Lactarius serifluus</i>	5.3	1190
(4) <i>Coprinus comatus</i>	5.3	1950
(5) <i>Boletus luridus</i>	2.8	1080
(6) <i>Merulius lacrymans</i>	2.0	720
(7) <i>Polyporus squamosus</i>	2.0	700
(8) <i>Polystictus versicolor</i>	0.5	280

* The "water content" referred to is the normal water content of these species, i.e. the amount of water in freshly gathered sporophores which have previously been growing under as nearly normal moisture conditions as possible.

Of the eight species tested, the four Agarics had considerably higher rates of respiration than had the four Polypores, and there appears to be some correlation between the amount of carbon dioxide evolved by, and the water content of, the fungi. Bonnier and Mangin (2) state that Agarics apparently respire at a higher rate than do Polypores, giving the rates of six species in the following order:

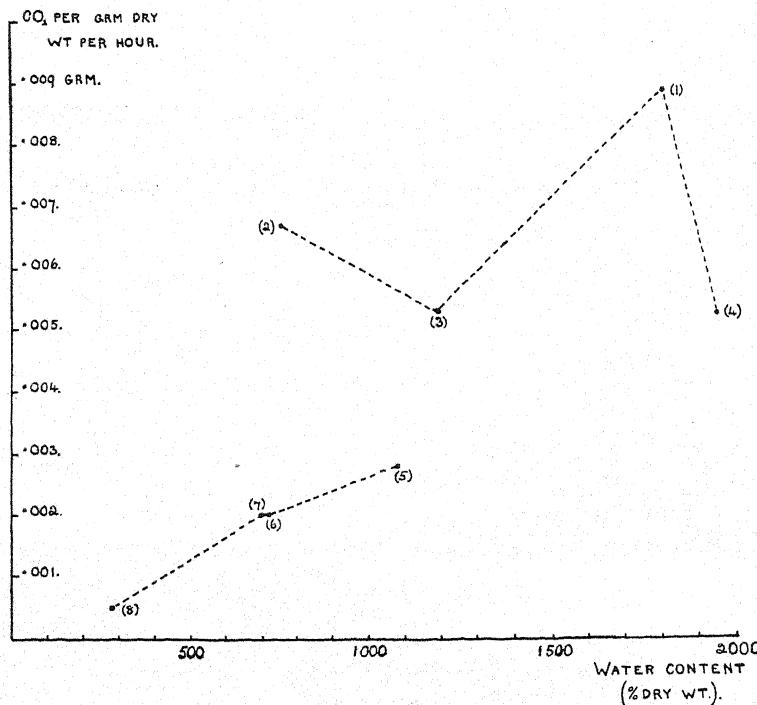


Fig. 4. Relation between rate of respiration and "normal" water content in the sporophores of various species of fungi (the numbers refer to the same species as those in Table I; numbers 1-4 are Agarics, and 5-8 Polypores).

(1) *Collybia velutipes*, (2) *Panus conchatus*, (3) *Psaliota campestris*, (4) *Trametes suaveolens*, (5) *Polystictus versicolor*, and (6) *Daedalia quercina*. They, however, did not observe the water contents of the sporophores they examined, but undoubtedly again those of the Polypores (all more or less woody or corky species) would be lower than those of the more fleshy Agarics.

The results obtained in the present investigations are shown graphically in Fig. 4, the numbering being the same as in the table above; it would seem better to keep the curves obtained for Agarics and Polypores separate. That given by the four Polypores is almost a straight line and indicates a marked correlation between water content and respiration. That of the four Agarics is less uniform, possibly because in this case we are dealing with very high water contents, and the "optimum" may be very different in different species—as was indicated previously in *Pleurotus ostreatus* and *Stereum hirsutum*. It is conceivable that some fungi may live normally under such conditions that their water content is actually above the "optimum" amount, and that the comparatively low rate of respiration of *Coprinus comatus* (No. 4) may be explained by its excessively high water content.

It would seem, then, that although the varying rates of respiration of different species of fungi cannot be traced solely to the amounts of water they contain, yet this factor is of considerable importance. These results may go some way towards explaining why, as Bonnier and Mangin state, the rate of respiration of fungus sporophores increases with the amount of moisture in the atmosphere. In saturated air, water is rapidly gained by the tissues; while in an unsaturated atmosphere, it is continually being lost; and the less the amount of water vapour present, the higher is the rate of loss. The rate of respiration will naturally respond to these changes in the amount of water in the tissues.

(3) *Water content and respiration in young and mature fungi.*

In three species, comparisons have been made between the rates of respiration of mature and young specimens (the young ones being still in the "button" stage). In all three cases, the mature and young sporophores were collected from the same crop, at the same time, and the experiments were performed under identical conditions. The results are given in the following table:

TABLE II

Species	Mature			Young		
	CO ₂ (mg.)	Ratio	H ₂ O cont. (%)	CO ₂ (mg.)	Ratio	H ₂ O cont. (%)
(1) <i>Polystictus versicolor</i>	0.5	—	285	0.8	—	245
(2) <i>Hypholoma fasciculare</i>	3.4	.85	1230	4.9	.80	1010
(3) <i>Lactarius serifluus</i>	5.4	.85	1150	4.5	.84	316

The rate of respiration is expressed as the number of milligrams of carbon dioxide evolved by equal weights of the mature and young specimens, in one hour; and the water content as percentage of the dry weight.

In the two first, the rate of respiration of the young specimens is decidedly higher than that of the mature ones, whereas the reverse is the case with *Lactarius serifluus*. These results are explicable when the amounts of water in the tissues are taken into account. In *Polystictus* and *Hypholoma*, the water content of the young sporophores was very slightly less than that of the older ones, while in *Lactarius* the difference was very pronounced. Thus the rate of respiration of young fungi, while depending primarily on the rapid rate of growth of the tissues, with the quickening up of metabolic processes caused thereby, is also dependent on the amount of water contained in the cells.

The value of the respiratory coefficient does not appear to change appreciably either with the age, or with the water content, of the fungi (*Hypholoma fasciculare* is a fungus whose ratio varies considerably in different individuals, and the difference of 0.05 in its value is well within the bounds of variation; in the case of *Lactarius serifluus* the two values, practically identical, are the means obtained from several experiments).

(4) Note on the water content of fungus sporophores.

Water content depends primarily on the balance between gain and loss of water. The most important factor in water-loss is evaporation from the exposed surfaces, and this in its turn must depend on many other factors. Such are (1) the hygrometric state of the air; (2) internal factors, such as thickness and composition of the hyphal walls, and the degree of compactness of the hyphae; and (3) the amount of freely exposed surface compared with the volume. Some observations have been made with a view to testing how far factor (3) can be said to affect the water content. In order to prevent factor (2) from masking this effect, as far as it is possible to do so, different parts of the same sporophore have been tested; it is almost impossible to attempt to compare one species with another. The results are given in Table III.

The calculated value for the surface area per c.c. of fungus material, in the cases of gills and tubes, is, of course, only approximate, and a large part of this area is more or less ineffective from an evaporation point of view, e.g. the surface lining the tubes of Poly-

TABLE III

Species	Portion	Surface area per c.c. Fungus material* (sq. cms.)	Water content (% of dry wt)
<i>Boletus luridus</i>	Tubes	300	820
	Flesh of pileus	0.87	2144
	Tubes + flesh		1144
	Stipe	1.31	1020
<i>Polyporus betulinus</i>	Tubes	47	360
	Flesh of pileus	0.53	420
	Tubes + flesh		400
	Stipe		
<i>Trametes odora</i>	Tubes	49	300
	Flesh of pileus	1.43	408
	Tubes + flesh		340
	Gills	36	370
<i>Pholiota squarrosa</i>	Flesh of pileus	1.43	430
	Gills	36	608
<i>Coprinus micaceus</i>	Flesh of pileus	2.50	614
	Gills + flesh		1670
	Stipe		2020
	Whole sporophore		1820

* The area and volume are calculated approximately from a few measurements. In the case of the pileus, small rectangular blocks from the central region only were used. The tubes, for the present purpose, may be regarded as cylindrical, while the gills are, approximately, prisms, with a triangular section.

pores. Although the water content is not affected proportionally by the variation in the ratio $\frac{\text{surface area}}{\text{volume}}$, yet we find that in each of the six species tested above, when this ratio is high, the amount of water is low, and *vice versa*. These results refer only to different parts of the same sporophores, yet it seems impossible to avoid the conclusion that differences in the value of this ratio between two species must be one of the factors determining the difference in their "normal" water contents. We have already seen that water content is one of the factors governing the rate of respiration of fungi; therefore the value of this ratio must also have an indirect bearing on the rate—the greater the relative area, the lower must be the rate of respiration, other factors being the same. But the ratio value must also have a direct bearing on respiration, owing to the freer access of air to the tissues in fungi which possess a large area. This direct effect will, of course, tend in the opposite direction to the indirect effect through the water content.

How does the quantity of water present in the tissues affect the rate of respiration? The answer to this question is probably to be found as the resultant of many physical and chemical effects. Although water is produced as the net result of respiration, yet it is essential

to, and absorbed in, the first or anaerobic phase. If there should be excessive water loss, so that in spite of its production by respiration and other processes, the total quantity in the system becomes low, then it is possible that this would directly affect the formation of carbon dioxide in the anaerobic phase. Again, in nearly dry cells, the colloids present are largely in the gel condition, and are practically solid; with the absorption of water they become sols, and, if water is very plentiful, may become so completely dispersed that many of the properties of true solutions are assumed. Another important manner in which water may influence the rate of respiration and other processes, is in connection with the dissociation of its own molecules, and those of the crystalloids present in solution.

(5) *Respiration and spore discharge.*

Several experiments have been performed on xerophilous fungi, to determine if respiration and spore discharge go hand in hand. Xerophilous fungi are defined by Buller(3) (p. 105), as species which, after being desiccated, when supplied with moisture begin again to shed spores. *Marasmius (Collybia) dryophilus* is one of the species mentioned by him. He found that it was able to recover after desiccation for one week, but failed to recover (i.e. shed spores) after a month. In these investigations, three sporophores of this fungus were gathered in a vigorous state, rapidly shedding spores, and their rate of respiration was tested immediately: they produced 4.7 mg. of CO₂ per hour. They were then dried in a current of air and allowed to remain in the desiccated state for one week. On soaking out (in a saturated atmosphere over wet filter paper) they began to shed spores after a few hours, and their respiration was again tested; it was found to have reached practically its former rate—4.5 mg. CO₂ per hour. They were again dried, and after another week moistened out once more. Spores were shed, but the respiratory rate was much diminished—1.2 mg. CO₂ per hour. After a further week of desiccation, these fungi failed to shed more spores on moistening, and only a trace of CO₂ was produced by them. The value of the respiratory coefficient in these experiments was practically constant—0.75 to 0.78.

Another specimen of *Marasmius dryophilus*, which had been collected and dried some months previously, was also soaked out. In this case no spores could be obtained, and a very small trace only of CO₂ was observed after a period of four hours in the respiratory chamber.

Many similar experiments have been performed on *Polyporus adustus*, and a similar result obtained each time. On repeated desiccation and moistening out, the value of the respiratory coefficient does not change, and the rate of respiration falls off at the same time as does the power of shedding spores. During the periods of desiccation, both processes practically cease.

Note on the effect of light on the respiration of higher fungi.

Bonnier and Mangin (2) state that diffuse daylight retards the rate of respiration of the sporophores of higher fungi, and that this retardation is most pronounced under the influence of the red and yellow rays, the blue and green having little effect; the respiratory ratio is unaffected by light. Purijewitsch (15) also obtained a greater rate of respiration of fungus sporophores in the darkness than in the light. Bonnier and Mangin found a similar effect with a mould, *Phycomyces nitens*. This species has apparently not been tested by other experimenters, but Elfving (11) supports their conclusion with other moulds, stating that in strong light there is some retardation of respiration in young cultures, though not with older ones. These results on moulds have been apparently contradicted by those of many other physiologists. Thus Kolkwitz (12), Maximov (14), Wilson (16) and Löwschin (13), experimenting with many species, have failed to find any retarding effect of light, though there is sometimes an accelerating effect, apparently due to the destructive action of light on various organic acids which accumulate in darkness. It would seem therefore that the results of Bonnier and Mangin concerning *Phycomyces nitens* are unreliable, which again casts a doubt on the reliability of the results of the experiments on higher fungi. In the present investigations, I have been quite unable to obtain evidence of a decrease in the respiratory rate in the light as compared with that in darkness.

Both electric and diffuse daylight have been used. The artificial illumination was provided by two Ediswan gasfilled "Fullolite" bulbs (60 watts), fitted with conical white reflectors, and distant about 10 in. from the respirating fungi. The daylight was not very strong, coming through a N.E. laboratory window, but it was increased by the use of suitably placed mirrors; the experiments were performed during the months of September and October, in the not very clear atmosphere of Birmingham.

Using artificial light, many experiments were performed on the two species *Marasmius conigenus* and *Polyporus adustus*; and with

daylight, on *Coprinus comatus*, *C. micaceus*, *Hypoloma fasciculare*, *Lactarius quietus*, and *Polystictus versicolor*. The fungi experimented on were all young specimens just before expansion, or just expanded. In none of these species was any significant difference obtained between the rates of CO_2 evolution in light and in darkness. In fact, the mean of the whole series of experiments gives a very slightly higher (though not significant) value for the rate of respiration in the light than in darkness.

Similarly, there is no evidence of any constant change in the value of the respiratory coefficient in these experiments. This was observed in eleven series of experiments; in six the ratio was slightly higher in the dark than in the light, while in five the reverse was the case. The means of the total numbers of determinations made in the light and dark are practically identical, 0.799 and 0.801 respectively.

It seems probable that the difference between these results and those of Bonnier and Mangin is not due to different species being used, since one (*Polystictus versicolor*) is common to the two investigations, and these experimenters give a marked difference between the rates of respiration of this species in light and in darkness. A possible cause of the difference is that the light used in the present investigations was not so intense as that used by the French experimenters; this however would not seem to account for the entire lack of any observable effect.

SUMMARY

1. In a given species of fungus (*Pleurotus ostreatus*, *Stereum hirsutum*, and *Polyporus adustus*) the rate of respiration of the sporophores bears a definite relation to the water content; respiration increases rapidly with the amount of water present. There is evidence, at least in two species, of an "optimum" water content; this is very high, particularly in the case of *Pleurotus ostreatus*.

2. As a general rule, Agarics respire at a faster rate than do Polypores; the rate appears to be more or less correlated with water content, at least in the case of those species which have low water content (chiefly Polypores). Among Agarics, other disturbing factors assume such dimensions that they conceal the connection between the two, if indeed it exists.

3. The rate of respiration of young fungi also depends largely on the amount of water they contain; this is usually slightly less than in mature specimens gathered from the same crop. The value of the respiratory coefficient does not change markedly with age.

4. The water content of different portions of the same sporophore varies, though not proportionally, with the value of the ratio $\frac{\text{volume}}{\text{surface area}}$.

5. In the case of xerophilous fungi which have been desiccated and later moistened again, respiration recovers so long as, and only so long as, spore-discharge also recovers. The value of the respiratory coefficient is unaffected by desiccation.

6. There is no evidence that the rate of respiration of fungus sporophores differs in any constant manner in darkness, from the rate when illuminated—either by diffuse daylight or by electric lamps. Similarly, the respiratory coefficient is the same in darkness as in light.

In conclusion, I should like to add my grateful thanks to Professor Yapp for his kindly help and criticism throughout the investigations, and to Dr Bayliss Elliott for providing much fungus material, and for her advice.

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THE REPRODUCTION AND DELIMITATION
OF THE GENUS *ZYGNEMA*¹

BY F. E. FRITSCH AND F. RICH

(With 2 figures in the text)

IT has long been customary to attach considerable importance to the location of the zygospore in the Zygnemaceae. Thus, in *Debarya* the gametes always meet in the conjugation canal and the zygospore is formed there, whilst in *Spirogyra* it invariably lies within the female cell. In *Zygnema*, however, both conditions are encountered. In species like *Z. pectinatum* Ag. and *Z. Ralfsii* De Bary the zygospores are formed in the conjugation canal, whilst in others (e.g. *Z. insigne* Kütz., *Z. stellinum* Ag.) they are situated in the female cell, and this difference is usually employed as a primary means of classification within the genus². Genera or species exhibiting production of zygospores within one of the conjugating cells also have been regarded as displaying physiological anisogamy, an interpretation which is warranted since, even when such forms undergo lateral conjugation, the zygospore is always lodged in one of the two cells involved and not, as in the case of the isogamous forms, in the canal.

Transeau³ in 1914 described a species of *Zygnema* (*Z. Collinsonianum* Transeau), from a pond in Illinois, in which the zygospores are formed either in one of the conjugating cells or in the canal. Although no mention of this fact is made in the actual diagnosis, it is practically the only marked feature that distinguishes his species from *Z. peliosporum* Wittr., which he recognises as closely related.

We have had the opportunity of examining abundant material of *Zygnema peliosporum* Wittr. collected by Miss M. Wilman and Mr C. Elliott Young in September 1921 and in September and October 1922 from diverse quiet pools in the Harts River, Newlands, Barkly West, Griqualand West⁴. The material collected by Mr

¹ From the Botanical Department, East London College, University of London.

² Cf. e.g. Borge, Zygnemales, in Pascher, *Süßwasserfl. Deutschlands, Österreichs, etc.* 9, p. 32, 1913.

³ Amer. Journ. of Bot. 1, p. 289, 1914.

⁴ This forms part of a large collection from Griqualand West which is at present under investigation.

Young in 1921 agreed in all essential respects with the descriptions given by Wittrock¹ and Borge², although of rather larger dimensions. The threads were $26-32\mu$ broad. The zygospores, which were invariably lodged in one of the conjugating cells (Fig. 1, F), though very often spherical, were not uncommonly broadly ellipsoidal (Fig. 1, E); some typical dimensions are as follows: 43×43 , 44×44 , 46×46 , 48×36 , 49×43 , $51 \times 37\mu$. In the mature condition the

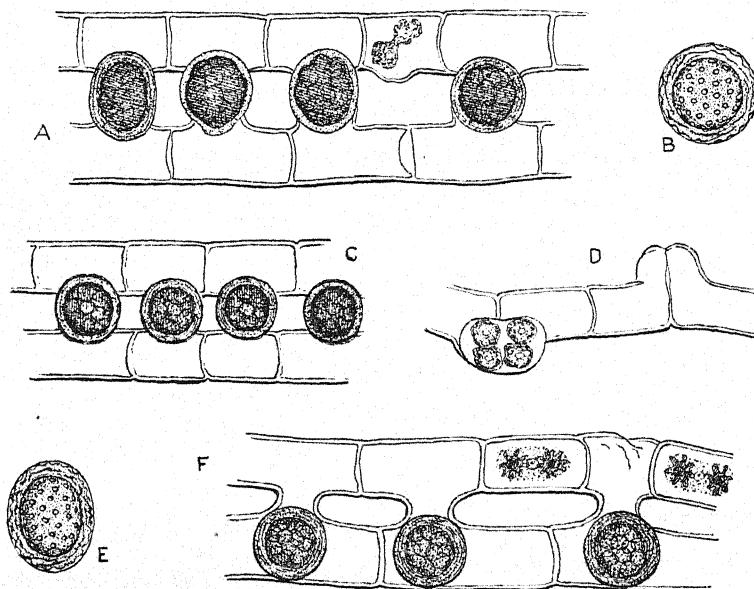


Fig. 1. *Zygnema peliosporum* Wittr. from Barkly West, Griqualand West. A-D, material collected in 1922 showing isogamous conjugation; B, single zygospore; D, lateral conjugation. E-F, material collected in 1921 showing anisogamous conjugation; E, single zygospore. (B and E $\times 340$, the remainder $\times 260$.)

thick middle layer of the zygospore membrane was of a dark greenish blue colour³ and provided with rather shallow and broad, fairly closely set scrobiculations (Fig. 1, E); the thin outer layer was smooth and colourless. The fructifying cells were slightly inflated on the side adjacent to the conjugation canal (Fig. 1, F).

On the other hand, in the material gathered in September and October of 1922 (partly by Miss Wilman and partly by Mr Young)

¹ *Bot. Notiser*, p. 188, 1868.

² *Loc. cit.* p. 36.

³ Scarcely "atro-violacea" as Wittrock describes it in his original diagnosis (*loc. cit.*).

the method of conjugation was of the other kind, practically all the zygospores being formed in the canal (Fig. 1, A, C); conjugation was either scalariform or, more rarely, lateral (Fig. 1, D). In one (but only in this one) of the seven samples, however, occasional filaments showed formation of the zygospores in the female cell, all the cells of a filament in such cases showing the same behaviour. The two diverse methods of conjugation were never observed in the same filament, as Transeau figures it (*loc. cit.* Fig. 1). Conjugation between several filaments was not uncommon. There can be no question that the 1921 and 1922 material belonged to the same species, since the material came from the same locality and there was absolute agreement in all respects except in the method of conjugation (cf. Fig. 1, B and E). The dimensions¹ of the 1922 material approached more nearly to those given by Wittrock. In view of the facts here given Transeau's species can scarcely be maintained, since there are no definite points of difference between it and *Z. peliosporum* Wittr. In our opinion *Z. Collinsianum* should be regarded as a synonym of the latter.

The case just discussed, however, raises the much wider question whether we are henceforth justified in regarding the point of formation of the zygospores in the genus *Zygnema* as a satisfactory feature for purposes of primary classification. If one and the same species can in a certain year exhibit the one method of conjugation and in another year the other method², the suspicion naturally arises as to whether this feature may be of as little systematic value in the genus *Zygnema* as the occurrence of scalariform or lateral conjugation is in *Spirogyra* or other members of Zygnemaceae. Possibly a better classification of *Zygnema* could be founded on the characters of the zygospores, their location being regarded as only of varietal value. In this connection attention may be drawn to the fact that the only marked point of distinction between *Z. pectinatum* Ag. and *Z. stellinum* Ag. lies in the position in which the zygospores are formed³. Are these two merely different forms of the same species, at one

¹ Diam. fil. 24–26 μ ; zygospores: when spherical 36–43 μ , when ellipsoidal 43 \times 32, 44 \times 32, 48 \times 34, 49 \times 27, 49 \times 29.

² In the case of *Z. spontaneum* Nordst. G. S. West (*Journ. Linn. Soc., Bot.* 39, p. 53, 1909) also records location of a few of the zygospores in the canal, although the majority were produced in the female cell. At the same point he expresses the opinion that *Z. Heydrichi* Schmidle (*Flora*, 84, p. 169, 1897), in which the zygospores are formed (by lateral conjugation) in the canal, is synonymous with *Z. spontaneum*. Here again then the place of formation of the zygospores is variable.

³ Cf. also *Z. Ralfsii* De Bary and *Z. leiospermum* De Bary.

time forming its zygospores in the canal, at another time in one of the conjugating cells? It is in order to focus attention on this point that this communication has been written.

A further point of interest lies in the occurrence of isogamy and physiological anisogamy in one and the same form, occasionally even in one and the same lot of material. Apparently *Z. peliosporum* is somewhat plastic as regards this feature and one may speculate as to what determines the one or other method of reproduction; external factors may to some extent be involved, since in the case above discussed the two types occur in the main in different years. In *Spirogyra* evidently physiological anisogamy has become fixed; is it really fixed in any species of *Zygnema*?

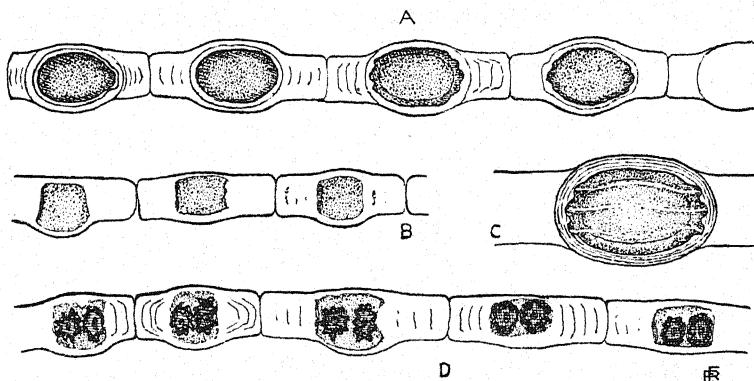


Fig. 2. *Zygnema fertile* n.sp., from Barkly West, Griqualand West. A, thread with mature azygospores. C, single spore, more enlarged. B and D, early stages in spore formation. (C $\times 450$; the remainder $\times 260$.)

In the same locality that afforded the above material there occurred another species of *Zygnema* which never exhibited conjugation, but occasional filaments were found forming azygospores of a very distinctive kind. We have named it *Z. fertile* n.sp.¹, because when azygospores are produced every cell of the thread is involved. The vegetative filaments are $20-22\mu$ wide, the cells being from $2\frac{1}{2}$ to 5 times as long; the cells have thin walls and there is a very slight (often scarcely perceptible) constriction at the septum. In the formation of the azygospores the contents contract to the centre of the cell which becomes inflated, either on both sides or only on one side (Fig. 2, B, D). At the same time the space left by the

¹ The full diagnosis will be given in the report on the collection of Algae from Griqualand West.

contracting contents at either end of the cell gets filled with opaque white-looking mucilage. The latter often shows distinct strata which either run parallel to the septa (Fig. 2, A, D) or appear as a series of thimble-shaped lines (Fig. 2, D, left). In the contracted protoplast the two chloroplasts with their pyrenoids are sometimes still distinctly visible (Fig. 2, D), but there is often considerable accumulation of fat which obscures them. The azygospores more or less completely fill the inflated portion of the cell and are usually appreciably longer than broad (31×41 , $31 \times 43\mu$, etc.); not uncommonly they have slightly protruded ends and appear somewhat barrel-shaped (Fig. 2, A). The mature azygospores (Fig. 2, C) are encased in a firm several-layered colourless membrane and are provided with a number of longitudinal ridges which appear as lines on the face of the spore, and as a number of knobs at the two ends. Many of the spores are misshapen. Threads of a hundred and more cells all showing various stages in azygospore formation have been found. It seems that by degrees the ends of the cells containing the spores round off (Fig. 2, B), with the result that the individual cells become free from one another.

There is considerable resemblance between this species and *Z. reticulatum* E. Hallas¹, where likewise only azygospores are known. The latter, however, are spherical and the middle layer of the spore membrane is yellow-brown and scrobiculate. Other marked peculiarities of this species lie in the fact that the chloroplasts usually undergo division (into as many as seven parts) prior to contraction of the contents to form the azygospores, and that the latter on germination produce from one to three new filaments². There is no mention of the mucilage being stratified in the case of this species.

Several other species of *Zygnema* are known in which formation of azygospores is frequent or the rule, viz. *Z. spontaneum* Nordst., *Z. Hansgirgi* Schmidle, and *Z. capense* Hodgetts³, but none of these show obvious accumulation of mucilage in the space left by the contracting contents. In the case of *Z. spontaneum* Nordst. the original

¹ *Bot. Tidskrift*, 10, p. 1, tab. 1 and 2, 1896.

² Kolderup Rosenvinge (*Rev. Algol.* 1, p. 209, 1924), owing to this feature, establishes a new genus (*Hallasia*) for *Z. reticulatum*, referring it to the Mesotaeniales and regarding it as intermediate between the latter and the Zygnemales.

³ Cf. also *Z. javanicum* v. Martens (de Wildeman, *Alg. Buitenzorg*, p. 113, 1900), which is incompletely known. Azygospores are also observed as an occasional phenomenon in species of *Zygnema* which usually produce zygospores. In view of what is known of *Z. spontaneum*, however, it is probable that these species may at times be found forming azygospores only.

material from the Sandwich Islands described by Nordstedt¹ had only azygospores, but W. and G. S. West subsequently recorded the same species from Angola² showing only zygospores (formed by scalariform conjugation). Still later G. S. West³ recorded the same species from the Yan Yean Reservoir with both azygospores and normal zygospores, in part even in one and the same filament. The two kinds of spores were identical except in dimensions. This species, therefore, again exhibits very considerable plasticity as regards its reproductive methods⁴. *Z. capense* Hodgetts⁵ is very similar, but the azygospores⁶ are formed at one end of the cell which is inflated at this point to accommodate them. Schmidle's *Z. Hansgirgi*⁷ is a very different form, the assignation of which to the genus *Zygnuma* is not beyond doubt. The azygospores have a brown membrane densely covered with somewhat truncate protuberances.

Z. reticulatum E. Hallas, which was briefly considered above, has been transferred to the genus *Debarya* by Transeau⁸, and no doubt he would also advocate a similar transference of *Z. fertile*. We are, however, altogether in disagreement with such a policy. Transeau (*loc. cit.* p. 18) gives the following three characteristics as distinctive of *Debarya*: "(1) the entire contents of the gametangia enter into the making of the zygospores; (2) the zygospore is formed in the conjugating tube and is not cut off from the other parts of the gametangia by partition walls; (3) as the gametes move toward the tube during conjugation, their place is taken by a secretion of cellulose, which renders the gametangia solid and highly refractive." The first of these features is characteristic also of *Zygnuma* and *Spirogyra*, the second, of several species of the former genus, while partition walls are not developed in any of the three genera here mentioned. There remains therefore, as the sole feature distinguishing *Debarya* from *Zygnuma*, the filling of the gametangia with refractive mucilage, and apparently every *Zygnuma* that shows this feature is to be transferred to *Debarya*. The nature of the chloroplasts, according to Transeau, is a matter of secondary importance⁹ and in the

¹ *Algae aquae dulcis et Char. Sandvicens*, p. 17, t. 1, figs. 23, 24, 1878.

² *Journ. of Bot.* p. 15, 1897.

³ *Journ. Linn. Soc., Bot.* 39, p. 52, 1909.

⁴ Cf. also footnote 2 on p. 204.

⁵ *Trans. Roy. Soc. South Africa*, 13, p. 66.

⁶ Hodgetts, Transeau, and others speak of these structures as "aplanospores," but this use of the term is altogether unwarranted.

⁷ *Hedwigia*, 39, p. 169, 1900.

⁸ *Ohio Journ. of Sci.* 16, p. 20, 1915.

⁹ Cf. *ibid.* 25, p. 194, 1925.

modified diagnosis of *Debarya* which he gives we have: "chromatophore varying from an axile plate with two or more pyrenoids to stellate chromatophores, each with a central pyrenoid¹."

It is possibly justifiable to regard the filling of the gametangia with mucilage as an important classificatory character within the genus *Zygnema*, but to make it the sole distinctive feature of a genus, overriding chloroplast characteristics, is surely introducing a very artificial element into the classification of the Zygnemaceae. The genus *Zygnema* is very well defined by its exceedingly distinctive chloroplasts, and occasional abnormalities do not detract from the value of this feature. Transeau² regards his *Debarya americana*, which has a two-lobed chromatophore with only two pyrenoids, as forming "an easy transition to the next species (*Debarya decussata* Transeau) in which the chromatophore resembles *Zygnema*." Only one vegetative cell of *D. americana* is figured³ and that on so small a scale that it is difficult to recognise details. The chloroplast is manifestly of a peculiar type, although not in our opinion showing much resemblance to that of a *Zygnema*. *D. decussata* Transeau is manifestly a species of the later genus.

SUMMARY

Material of *Zygnema peliosporum* Wittr., gathered in Griqualand West, has been found at one time to exhibit formation of the zygosores in the canal, at another time in one of the conjugating cells. The importance of these phenomena is discussed. *Z. Collinsianum* Transeau is regarded as synonymous with this species.

A new species of *Zygnema* (*Z. fertile*) producing azygospores is described and other similar cases are discussed.

The reference by Transeau of species of *Zygnema*, exhibiting accumulation of mucilage in the conjugating cells, to the genus *Debarya*, is regarded as artificial and obscuring real affinities.

Note. Since writing the above we have received a paper by H. Skuja (Act. Hort. Bot. Univ. Latviensis, 1. p. 109, 1926) in which a new species of *Zygnema* is described (*Z. synadelphum* Skuja). In view of what we have communicated, we are of the opinion that this species is but a form of *Z. peliosporum* Wittr.

¹ *Ohio Journ. of Sci.* 16, p. 20, 1915.

² *ibid.*, 16, p. 19, 1915.

³ *ibid.*, 25, Pl. I, fig. 17, 1925.

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STUDIES IN THE ECOLOGICAL EVOLUTION OF THE ANGIOSPERMS

By J. W. BEWS, M.A., D.Sc.

CHAPTER IV TREES AND SHRUBS

INTRODUCTION

THE CLASSIFICATION OF PLANT FORMS

THOSE who have dealt with the classification of plant forms (growth forms or life-forms) have hitherto paid little attention to their ecological evolution or, in other words, to their arrangement on phylogenetic lines. The systems adopted by the earlier writers, e.g. Humboldt (1806) and Grisebach (1872), were purely physiognomic. Drude (1890, 1913) has laid stress on two principles, viz. the functional rôle played by any species in vegetation, and its life-history under conditions prevailing in its habitat, with particular reference to duration, protection and propagation. Warming's system (1909) follows similar lines, and in addition he laid stress on "Habitat forms" i.e. general reactions to habitat conditions, particularly to the water factor. Clements, in his later work (1920), states that much the most useful and consistent view of life-forms is obtained from a single point of view—that of vegetation and dominance, and he arranges his different classes of "vegetation forms" more or less in the order of the usual plant successions, beginning with annuals and ending with trees. This arrangement, however, as will be shown more fully later, is more or less the reverse of a true phylogenetic arrangement. Species which appear early in the plant successions are usually modern highly developed forms.

Raunkiaer (1910) by laying stress on the importance of the responses to the resting season, formulated a system which comes nearest to being a truly phylogenetic system, though he himself does not regard it from this standpoint. His class of Phanerophytes or woody plants comes first, and he ends with the highly evolved

Therophytes or annual plants. But he falls back in part on a habitat classification and his Helophytes (or marsh plants) as well as his Hydrophytes (or aquatic plants) are not placed in their proper position in an evolutionary scheme of classification. A more important defect in his system is that he did not give value to the effects of the biota. Climbing plants, for instance, he includes among Phanerophytes.

From the standpoint of comparative anatomy, the work of Jeffrey (1917), Sinnott and Bailey (1914) and others lends strong support to the view that, among the Angiosperms, woody types are more ancient than herbaceous. Sinnott and Bailey have also considered the evidence from phylogeny and geographical distribution in support of the view that the tropical woody vegetation is, in general, older than the temperate herbaceous.

In my former work dealing with the vegetation and plant forms of South Africa (1925) the evidence from phylogeny and distribution was examined in some detail, and in addition the concept of primitive unchanging types of habitat as contrasted with more derivative non-persistent types was developed. It was considered reasonable to suppose that the moist-tropical vegetation of Africa, which had apparently remained under its present conditions for a vast period of time and showed connections with the tropical flora of America and Asia, was in general older than the specialised and often xerophytic flora of South Africa. Hygrophilous marsh and stream bank types were also considered relatively old, as well as some seashore types. The mountain ranges were indicated as relatively persistent (at least in the African continent) and the mountain African flora was regarded as a relatively ancient temperate type.

With the evidence from palaeobotany, phylogeny and distribution as set forth in condensed form in the previous chapters, it is now possible to apply those ideas to the world's flora as a whole, and attempt an analysis of the general course of ecological differentiation among the flowering plants, and, as a consequence, the phylogenetic classification of the Angiospermous plant forms. The general lines to be followed by this analysis have already been foreshadowed.

DIFFERENTIATION UNDER MOIST-TROPICAL CONDITIONS

While moist tropical conditions are relatively constant and unchanging, it must not be assumed that they are absolutely so. Even in tropical rain forest there are some brief periods of relatively drier conditions. Throughout the long past history of our present

moist-tropical vegetation it is extremely likely that changes in the inorganic environmental factors have played some part in its ecological differentiation. Otherwise the dominant trees would probably be of a more uniform type even than they are.

The most important factor, however, which has led to the present richness of the tropical flora has been simply the great lapse of time, combined, of course, with the constant effects of plant competition for space and the biota generally.

There may be something in the idea that favourable conditions in themselves, and apart from the time factor, have led to increased differentiation, that it is when the environmental conditions are as near the "optima" as possible that new species arise most easily, owing to that initial impulse to vary, about which we know so little. Such hypotheses, however, are largely speculative, and very hard to prove. The full extent of the ecological differentiation under uniformly favourable, warm, moist conditions has already been outlined. Trees, subordinate shrubs, lianes, epiphytes and herbs, as well as parasites, saprophytes and peculiarly specialised insectivorous plants have all been produced.

TREES AND SHRUBS AND THEIR ECOLOGICAL EVOLUTION

The responses to drier and colder conditions have been shown to be, in general, more recent. In the arrangement of our subject-matter in this and the succeeding chapters, the modern vegetation types might have been dealt with in turn, e.g. tropical rain-forest, forest and scrub of drier subtropical, and of temperate regions, grassland vegetation, tundra vegetation, desert vegetation, etc. Constant reference will have to be made to the great geographical climatic areas, in any case, as well as to more specialised habitats, and to the types of vegetation which occupy them. But perhaps the best way of approaching the subject of ecological evolution is to make the plant forms themselves and their evolutionary history the main basis for the arrangement of the facts, and the phanerophytes or trees and shrubs will be dealt with in this chapter.

The trees of moist tropical forest, according to all the evidence already put forward, are to be regarded as the most primitive of Angiosperms. It is therefore important to have clear ideas regarding their main characteristics since they supply the starting-point in the evolutionary history of the more modern types of plant form.

THE GENERAL CHARACTERS OF TREES AND SHRUBS OF THE
MOIST TROPICS

1. Owing to the great lapse of time and the effect of internal factors, as well as under the influence of the biota and, to a much less extent, variations in the inorganic environment, differentiation among tropical trees of moist regions has proceeded very far. Floristically this is shown by the long list of families to which they belong. Only the most important need be mentioned, viz. Moraceae, Ulmaceae, Olacaceae, Anonaceae, Monimiaceae, Myristicaceae, Lauraceae, Leguminosae, Simarubaceae, Celastraceae, Anacardiaceae, Icacinaceae, Sterculiaceae, Tiliaceae, Guttiferae, Flacourtiaceae, Lecythidaceae, Rhizophoraceae, Combretaceae, Myrtaceae, Araliaceae, Myrsinaceae, Sapotaceae, Ebenaceae, Oleaceae, Rubiaceae. Ecologically, their forms also vary to some extent, though on the whole, they are fairly uniform. They differ in height, they differ in the shape and size and texture of their leaves within certain limits, as well as in other form characters.

2. Flowers and reproduction. The general long-continued uniformity of environmental conditions and the absence of any response to a pronounced resting season are to be correlated with the lack of any marked contrast between the vegetative and the reproductive life of the species. Growth goes on uniformly and steadily more or less all the year round, though there are certain irregular growth rhythms that are not well understood, that are not necessarily synchronous for the different species, and have no relationship to seasonal changes. The period of flowering is far more erratic among the trees of moist-tropical forest than elsewhere. Though many, perhaps even the majority, have more or less fixed periods of flowering, the exact time varies greatly among the different species. Many species, on the other hand, flower at any time of the year. The lack of marked contrast between the vegetative and reproductive life of the species extends also to the spatial relationships between the two, though this applies, to some extent, to more derivative types of trees as well. The flowers of tropical trees are produced in any position, even on the older parts. There is, as a rule, little attempt at localisation. Single flowers or small clusters are common. There are few large conspicuous, dense inflorescences. The evolutionary history of the branching of inflorescences should be analysed in greater detail for the Angiosperms as a whole, but it is among herbaceous and other derivative forms that the more highly evolved types occur.

The phenomenon of cauliflory in tropical trees will be referred to in connection with the characters of their bark.

As regards the influence of the insect world on the form of their flowers, a very common idea prevails that the tropical tree flora is one with flowers more brightly coloured, more showy and conspicuous and generally better adapted to insect visits than those of temperate regions. This is entirely a mistake. A glance through the list of families given above should be sufficient to convince the botanist that conspicuous flowers are very rare indeed. Where such do occur in tropical rain-forests, they belong, as a rule to derivative types, lianes, epiphytes and herbs. Even such derivative types are not floristically so conspicuous as many think. Wallace in his *Essays on Tropical Nature* says, "Conspicuous masses of showy flowers are so rare that weeks or months may be passed without observing a single plant worthy of admiration." "My friend, Dr Richard Spruce, assured me that by far the greater part of the plants gathered by him in equatorial America had inconspicuous green or white flowers."

The main characters of the fruits and seeds of moist-tropical trees must be dealt with briefly though the subject is full of interest. If dispersal is by external means then fleshy fruits and animal dispersal are the rule or the fruits or seeds simply drop from the trees, and are not distributed by any external agency. Wind dispersal could not, in any case, prove very effective in dense tropical rain-forest. The resting period of the seeds is apparently usually a short one, though more exact information on this subject is needed. Guppy believes that vivipary is a primitive characteristic and was at one time more or less universal, but the modern mangrove flora hardly supports this view, since in all other respects than their vivipary the mangroves are rather a specialised and derivative group, consisting of 25 species altogether, belonging to a variety of distinct families which, with the exception of one palm, are all rather advanced members of the Archichlamydeae or of the Sympetalae. Neither floristically nor ecologically (except possibly in their vivipary itself) are the mangroves to be considered primitive.

3. The absence of a pronounced resting season is reflected in the characters of the wood. The trees of tropical rain-forest belong mostly to the "hardwood" class. Many of them have very dense hard woods with a specific gravity greater than 1, so that they sink in water. Now this extreme hardness is impossible in woods where more abundant storage elements are required. The woods of

the drier subtropical regions with long, dry winters are, as a rule, much softer and lighter, as are also the woods of temperate trees, though the mechanical elements developed in trees growing in more exposed situations may lead to toughness and "strength" or resistance to tensile stresses. Hardness and toughness of course are not necessarily interconnected in woods. If a single character is needed to serve as a basis for subdividing this fairly uniform class of plant forms, relative hardness in the wood is about as convenient and suitable as any. A considerable amount of information on this subject is already available in the literature dealing with forestry. Increased softness in the wood is correlated with increased storage in response to colder and drier seasons which, as we have seen, has meant, in general, evolutionary advance. Owing to the fact, however, that mechanical elements are well developed in the species which grow more isolated and more exposed to the force of winds, the correlation between relative hardness and softness and the absence or presence of storage tissue in the wood is not necessarily a very exact one. Even granting this, one may still at least maintain that the characters of the wood are probably most suitable for the purposes of ecological subdivision of evergreen tropical trees rather than more superficial characters such as those of the leaves or bark or methods of branching, etc.

4. The trunks of tropical rain-forest trees are not usually so stout as those of equal height growing in more open situations. They grow very tall but remain relatively slender and, as a rule, they require additional support near the base. This is secured by means of plank buttresses or stout cylindrical roots, springing from the stem some distance above the base.

5. Branching. The trees of moist-tropical regions are very sparingly branched. Frequently there are only three grades of branching with the leaves aggregated in tufts at the ends of long bare axes. The number of grades of branching hardly ever exceeds five whereas the trees of temperate and drier regions frequently have seven or eight.

6. The bark of tropical rain-forest trees is thin and poorly developed, sometimes almost transparent, so that the chlorophyll of the cortical layers is visible through it. The absence of a thick bark allows the axillary flower buds to remain dormant for several or many years and then develop, producing flowers on the older parts of the twigs or stem, the phenomenon known as "cauliflory." Wallace explained cauliflory on teleological lines as an adaptation for pollination by shade-loving Lepidoptera, which do not fly above the canopy

of the forest, but it is doubtful whether there is any need for such explanations.

7. Thorn development is very rare, but not altogether absent from tropical rain-forest trees. It occurs in species of *Xanthoxylon*, as well as among subordinate forms such as certain palms. It is a phenomenon which increases to such a marked extent under drier conditions that the fact that it occurs at all under rain-forest conditions is important and requires special emphasis.

8. The buds of moist-tropical forest trees have rarely, if ever, any covering of dry bud scales, but there is a certain amount of protection by means of stipules, leaf sheaths, or outgrowths of the petiole. There is also often excretion of water, mucilage or resin between the bud and its envelope. Schimper gives further details and refers also to the peculiar phenomenon of flower-buds being immersed in water or containing water in their calyces until shortly before their anthesis. The lack of very much bud protection is generally to be correlated again with the absence of a prolonged resting season. Whether the possession of rather loosely arranged "naked" buds has any effect on the leaf shape is uncertain or doubtful.

9. Leaves. Large, simple, smooth-margined, leathery leaves are the commonest type. Compound leaves also are found, but the percentage of compound leaved forms tends to increase markedly in the drier subtropical region. The most important fact is that the leaves are "evergreen," i.e. they last for more than a year, so that the tree, except in rare cases or under exceptional circumstances, is never leafless and the work of assimilation can be carried on without interruption throughout the year.

The prevalent leathery texture and other xerophytic characters of the leaves of moist-tropical trees have already been discussed in the first chapter (pages 15—19) in connection with the fossil Angiosperm flora, where the same features were common and characteristic. It was shown to be correlated with relative inefficiency in water conduction through the wood. It may be mentioned in passing that this supplies another argument in favour of using the anatomical characters of the wood as the basis for further subdivision of this class of growth forms.

Apart from their xerophytism, the structure of the leaves of rain-forest species must be correlated in general with their evergreen habit and their relative durability. They carry out their functional activities for a much longer period of time than deciduous species. They are built to endure.

Various teleological explanations of the structural features of rain-forest leaves have been put forward by previous writers. Their coriaceous texture has been supposed to have the purpose of preventing mechanical injury from the very heavy rainfall; such devices as a smooth cuticle, drip tips, channelled nerves and velvety leaves with papillae (the latter chiefly among the undergrowth) have been thought to prevent wetting of the surface and the growth of epiphyllous algae, lichens, fungi and liverworts. Hydathodes are supposed to facilitate water excretion, and to prevent injection of the intercellular spaces of the leaves. Such views were put forward by Stahl, Haberlandt, and Schimper and many others have followed them. They illustrate very well the attitude of most botanists during the years which followed the enthusiastic reception of the principle of natural selection.

The explanations are plausible and likely, yet they are pure guesses, and no attempt was made by those who originated them to connect them with the normal basic physiological processes. Shreve (1914) carried out experimental work in different directions in the montane rain-forests of Jamaica and failed to confirm the view of Stahl that dripping tips facilitate the drying of leaf surfaces. Epiphyllae he found abundant on leaves of every type including those with drip tips. Hydathodes and other supposed adaptational features, Shreve also found, failed to perform the functions attributed to them.

DIFFERENTIATION UNDER DRIER AND COLDER CONDITIONS

The derivative vegetation of drier and colder regions shows a much greater range of diversity than that of moist tropical regions. This briefly may be considered as due to the following reasons:

- (a) The internal forces, which lead to differentiation independently of the environment, continue to act.
- (b) There is increased diversity of the inorganic environment, and the plants have reacted thereto.
- (c) The effects of the organic environment are still seen, but, in so far as plant competition for space is concerned, this is of decreasing importance the more the forces of the physical environment come into play.
- (d) The derivative flora has not had a single point of origin or even a few, but has been continually added to by the already rather highly differentiated more ancient, moist-tropical flora. It may be recalled that it was chiefly in the narrower circles of affinity that the

warm, hygrophilous types were shown to be phylogenetically more primitive than the types adapted to colder and drier conditions. The latter reflect the varying degrees of differentiation previously undergone by their ancestral forms. The whole problem, therefore, is rather complex and there is a real danger of serious error arising when an effort is made to fit the facts into a single cause and effect relationship between climate and vegetation, as has so often been done. Progress is only possible by continued and careful comparisons of all different types from every different standpoint both physiological and morphological and by paying attention to phylogenetic history as well as to the reactions and ontogeny of the species.

The physiological facts are the most fundamental. Of course changes of form and structure go hand in hand with changes of function, and form and structure are more easily studied, but Osborn (1925) is probably right when he insists that the ancient dictum of Aristotle holds good, that "Change of function precedes change of form." Function is a more labile thing than form. It is always difficult to separate the two and the study of so-called pure physiology may lead to the adoption of as narrow views as the study of morphology by itself; but teleological reasoning is now generally condemned even though it is difficult to avoid it altogether. It should be supported by experimental work wherever possible.

It is well known that species vary, that the individuals belonging to a species are not all alike. The species of the systematist, moreover, is often found to be made up of smaller units (microspecies, varieties or races). In this connection during recent years a good deal of comparative physiological field work has been carried out in Natal (Bews and Aitken, 1923, 1925). Comparative measurements have been made of the aeration systems of different species, of their transpiration rates, of their water requirements and water deficits at different seasons and under varying conditions, of their rates of water-conduction, etc., combined with examinations of their structural modifications. The result of it all has been to indicate that very likely physiological races may be recognised, which do not differ in, at least, any very obvious or easily recognisable structural features. Species (e.g. *Ptaeroxylon utile*) may grow in mesophytic or even hygrophilous forest or may be found outside the forest in extremely xerophytic situations. A long series of experiments, carried out by Aitken, showed that this species, as represented in the drier parts, possessed a remarkable power of lowering the water content of its leaves (i.e. of tolerating a high water deficit) without

injury. It is very difficult to be sure that structural modifications are not involved but it can at least be said that physiological processes apparently change without any obvious changes of structure.

Our experiments showed further that, while the species which appear relatively late in the plant succession are usually very rigid in their requirements and show a small range of variation in their physiological processes, the species which act as pioneers or appear early in the plant succession are much more plastic physiologically. But the climax species belong to more primitive types of plant form than the pioneer species. An increase of physiological plasticity, therefore, has been one of the trends of evolutionary development.

The first evolutionary change shown by primitive tropical species was probably the initiation of the process of acquiring this greater degree of plasticity in their physiological behaviour. Structural changes followed. A long time probably elapsed before the various efficient modern types of plant form were produced. Important alterations took place in their anatomy, in the characters and arrangement of the conducting elements, in their storage tissues, etc. as has fully been recognised by Jeffrey and others, whether they are right or not in the details of their analyses of the order of the changes.

The main contribution which can be made to this subject by our present studies in ecological evolution consists of a comparison of the moist tropical types already described with the types adapted to drier conditions on the one hand and to colder conditions on the other. Since the latter are both relatively modern forms the differences illustrate various evolutionary trends. Reactions to drier conditions and to colder conditions have much in common. In both cases it is the necessity of providing for a resting season that has led to the most fundamental changes. But there are also differences between the reactions to the different main types of climate. As a matter of fact, the subdivision of the derivative types can be carried rather far, but our space is limited and only three main evolutionary trends will be dealt with here, as follows:

- (1) The responses seen in the trees and shrubs of tropical and subtropical regions with dry seasons, culminating in the extreme types of woody xerophytes found in desert regions.
- (2) The differentiation of warm temperate sclerophyllous vegetation occurring in regions of wet winters and dry summers.
- (3) The differentiation of other temperate woody vegetation.

EVOLUTIONARY TENDENCIES IN THE TREES AND SHRUBS OF DRIER
TROPICAL AND SUBTROPICAL REGIONS (REGIONS WITH DRY WINTER
SEASONS, SEMI-DESERTS AND DESERTS)

1. Floristically the families represented are more advanced. This has already been sufficiently emphasised in the preceding chapters.

2. Flowers and reproduction. The well-marked seasonal growth rhythm is reflected in the increased localisation in time and, to some extent, in space, of the reproductive processes. The majority of the species flower in spring at the beginning of their new period of growth. Conspicuous flowers are more common, especially among shrubby forms. Wind dispersal of fruits and seeds becomes fairly common. The seeds are more viable.

3. The woods of the trees and shrubs in regions where there is a pronounced dry resting season show a much greater range as regards hardness. A few are fairly hard, but the majority are much softer than the woods of moist-tropical forest trees. The increased softness is chiefly to be correlated with the development of parenchymatous storage tissue in the wood.

4. There is a general reduction in height among derivative forms which reflects fairly accurately and proportionately the increasing aridity, though, in the previous history of the various species, the action of the biota may have been partly responsible for bringing it about. There is not, however, a proportionate decrease in the diameter of the stems with decrease in height. On the contrary, trees growing in more open situations usually have widespread branches and foliage and much stouter trunks than those of tropical forest. This is usually explained as a response to the light factor (which is, of course, important). But it is explained more comprehensively by reference to the effects of the biota generally. Tropical species grow tall and slender because success in plant competition depends more than anything else on ability to grow tall. With decreasing effects of the biota trees grow as large as possible but not necessarily as tall as possible. Of course there is a limit to the size they can reach even under favourable conditions and in the absence of competition, depending largely on the mechanical difficulties of their organisation, but this limit, in the case of many spreading giants of subtropical regions, is a rather high one.

Since the stems of trees in more open situations are stouter, there is not the same need for extra support and buttresses, supporting roots, etc. are not as a rule developed.

5. Decrease in height is usually associated with increase in branching. In many forms the branching takes place a few feet above ground, giving a short trunk and a very spreading, umbrella-like canopy—the "flat-crowned" type characteristic of open savannah forest in subtropical regions. It is a form well suited to withstanding winds but very badly adapted to withstanding the weight of snow. Snowstorms occasionally occur in Natal and I have somewhat vivid recollections of the absolute devastation caused by a not very heavy fall of snow among the flat-topped trees of the Thorn Veld (*Acacia* spp. dominant).

6. With further decrease in height combined with increase in branching the tree form passes into the shrub form. A continuation of the process produces dwarf-shrubs, suffrutices, under-shrubs and finally herbs. Even within the limits of a single genus (e.g. *Euphorbia*, *Hibiscus*, *Solanum*, etc.) the whole range of forms may be found. The lower-growing shrubby and herbaceous derivative types will be dealt with in greater detail later.

7. There is a general decrease in size of the leaves with increasing aridity which, on the average, is very well marked but is not quite universal. Hereditary influences play a part and a few trees of open forest have large leaves. (See statistical comparisons given in the first chapter.)

8. The percentage of species with compound leaves tends to show decided increase, with increasing aridity. Since the separate leaflets are the assimilating units, leaf division has more or less the same effect as reduction in the size of the leaves.

There have, however, been many teleological guesses at the significance of compound leaves. Schimper refers to their mobility and Cowles (in vol. II of the Chicago Textbook, p. 551) supposes that divided leaves are peculiarly favourable for the sifting of sunlight and for increasing the aggregate surface illuminated. Apart from the fact that no proof is offered for such hypotheses, the evidence already mentioned that leaf division tends to increase among types occupying open sunny situations would tell against the suggestion put forward by Cowles. It is the trees of dense tropical forest that require to increase as much as possible the aggregate amount of illumination, not the trees which grow in the open, fully exposed to full tropical sunlight.

9. Leaf-fall. This is one of the most obvious of the external signs of a seasonal periodicity. In the regions of dry winters the deciduous tendency varies among different species and among individuals of

the same species. Though it involves structural changes, leaf-fall is quite comparable with the physiological processes already discussed, which vary without any very apparent corresponding morphological changes, and it is interesting to find that here also some species or races are far more plastic than others. The primitive moist-tropical forms, as we have seen, sometimes show irregular deciduous tendencies.

10. Where the deciduous habit has become fixed, it is correlated with changes in the architecture of the leaf. Deciduous leaves are not built to endure. They are thinner and flimsier and usually have straighter main veins than evergreen leaves. The changes undergone in preparation for the actual process of leaf-fall itself are well known and need not be described in detail. But a very useful piece of work would be a more detailed comparison, both physiological and morphological, than has so far been undertaken, of the deciduous and evergreen types of leaves.

11. Bud-protection especially in the case of foliage buds is more pronounced in the drier regions than in the moist tropics. Bud scales are often present and are sometimes very thick and well developed.

12. A thick bark is a common feature of the relatively more xerophytic tropical and subtropical trees, forming a marked contrast with the thin smooth bark of moist-tropical forest trees. Priestley and Woffenden (1922) quote Douliot as calling attention to the marked effect of light on the formation of periderm in the stem. Priestley (1921) also refers to work carried out in his laboratory on the rôle played by sunlight in causing the rapid condensation of phellonic acid, one of the suberogenic acids concerned in cork formation, but he is inclined to attribute increased cork formation under increased insolation to the more rapid evaporation from the stomata and the consequent early blocking of the sub-stomatal apertures. The blocking is followed by accumulation of sap which is followed again by the appearance of a meristematic phellogen.

Whatever the underlying causes, there is no doubt that extensive cork formation is favoured by the open sunny situations which are occupied by the derivative subtropical trees. Constantly recurring grass fires, which, without doubt, are often caused by natural agencies, and have, therefore, been a factor of some importance ever since the establishment of extensive areas of grassland, are also said to cause increased cork formation in woody species occupying grassland habitats. Whether this direct effect of fire has in course of time become hereditarily fixed is, of course, much more difficult to prove and would, by most botanists, be considered unlikely.

13. Lignification from the physiological standpoint is still a very obscure process. The importance of lignified tissues in giving strength and rigidity is sufficiently obvious and is dealt with very fully in such works as that of Haberlandt. More attention might with advantage be directed to the phylogenetic aspects of physiological anatomy, but we can hardly enter into a discussion of the subject here. According to Jeffrey's ideas lignified tissues in the stem (the tracheids) have, in the course of time, been transformed into storage parenchyma. Increased storage is, of course, one of the most important results of a dry resting season and, as we have seen, often leads to the production of a softer type of wood.

On the other hand, there is an increase of lignification in the leaves of many evergreen xerophytic forms. It has been suggested by Guttenberg (1907) that increased lignification in leaves plays an important part in preventing deformations of the cells and softer tissues. It also prevents fatal injury when the water deficit is increased. Experiments carried out in Natal (Bews and Aitken, 1923) have shown that there is a rough agreement between increased lignification in leaves and a slower rate of drying out, though the agreement is not altogether a close one and doubtless other forces are at work as well. Increased lignification, as a rule, goes hand in hand with decrease in size of the leaves culminating in the ericoid form which, though it occurs in drier subtropical regions, is more characteristic of mountainous and temperate vegetation. Increased lignification among xerophytic tropical or subtropical types often results in a complete transformation of the organ concerned, and a loss of the original function in the production of thorns.

14. Spinosity. Thorn development, as already mentioned, increases more or less in direct proportion to increased aridity. In many desert regions practically all the woody species are thorny. But species are usually very plastic in this respect, as plastic as they happen to be in their water requirements. A few species may even be entirely thornless or very thorny according to the situation in which they grow. Lothelier's experiments (1890-3) have shown that in moist air or in feeble light normally thorny species like *Ulex* can become leafy and thornless.

When there is increased vigour of growth as on coppice shoots or when thorny species are kept cut back and there is, in consequence, an increased water supply to the shoot system from the relatively large root system, then the thorns are often much larger and more prominent than usual. While thorn development may be regarded

as the final visible result of the increased lignification which appears to result from increased aridity, a full understanding of the cause of their formation will probably have to await a better knowledge of the process of lignification itself. But from the natural selection standpoint there is no doubt that the presence of thorns serves to protect plants against grazing herbivores. Botanists, however, as already pointed out, are no longer completely satisfied by such teleological explanations.

15. Succulence. From the physiological standpoint more attention perhaps has been paid to succulence than to any of the other evolutionary trends among Angiosperms, especially by Dr Macdougall and his associates, e.g. H. A. Spoehr in his elaborate researches on the carbohydrate economy of the Cacti. The pentose series of sugars, though present in varying amounts in all plants, constitute, at times, more than half the total sugars of the Cacti. While the simpler sugars decrease with drying, the pentosans increase decidedly. Researches of this kind are, of course, of fundamental importance. Moreover Macdougall's dendrograph records show that daily variations in the size of the stems of succulents are approximately the reverse of those occurring in woody trees and most herbaceous plants. Swelling begins in succulents in mid-forenoon while the stomata are closing and continues until nearly midnight, when the stomata open. After midnight contraction sets in and continues until forenoon. Ecologically succulents are characterised chiefly by their large water balance on which they draw during dry periods. There are, however, few tree succulents; the Cacti in America and the genus *Euphorbia* in Africa are the best known examples. The vast majority of succulents are more or less herbaceous. All succulents are highly evolved not only ecologically but also floristically.

16. Increased osmotic pressure in the cell-sap is an important feature of plants of drier regions and especially of desert plants as has been shown by the work of Fitting (1911), of Iljin, Nazarova and Ostrovskaya (1916), and of Harris and various co-workers in America (1916, 1917). The last mentioned have published numerous important papers on this subject.

17. Minor xerophytic features among this derivative class of plant forms need not be dealt with in detail, e.g. protection to the stomata, coverings of leaf-surfaces, etc. Most of them have been explained on teleological lines, but there is room for much further experimental work, which might throw light on their relationship

to the basic physiological process and on their origin and evolutionary history in each case.

SCLEROPHYLLOUS VEGETATION

The type of vegetation termed "sclerophyllous" by Schimper is found in the Mediterranean region, in California, in the south-west of South Africa, in the south-west and south of Australia and in Chile. In general it is a type adapted to wet winters and dry summers, but both in America and in Africa it tends to spread along the mountain ranges into regions of wet summers. It differs chiefly from the vegetation of regions with dry winters or very cold winters in being evergreen. Though derivative, it is in many respects an older type than that of dry winter regions. It is separated from the moist-tropical by a wider gap. It contains many floristic elements that do not connect very closely with tropical types, e.g. Proteaceae, Ericaceae, etc., though in other cases its tropical origin and derivative character is clearer, e.g. in the Compositae, Leguminosae (Papilionatae), Rosaceae, Geraniaceae, etc. Trees are rare, but those that do occur have closer tropical affinities than the typical Macchia shrubs, e.g. *Olea*, *Laurus*, *Ocotea*, *Olinia*, *Gymnosporia*, etc. Its general floristic composition and connections with the primitive allied tropical types have been mentioned in the survey of the families given in the previous chapters. There are many indications that it represents the earlier responses to temperate conditions, and began on the mountain ranges of the world probably as early as Cretaceous times.

The climate of the regions with sclerophyllous vegetation possesses the following features. The winters are mild; frosts, if they occur, are not severe and only at higher altitudes does snow fall. The rain falls mostly in winter, but the rains though heavy are not of long duration. There are plenty of intervals of bright sunshine and growth can continue throughout the winter. The summers are much drier, but growth does not cease in the dry season, since there is still a supply of water in the soil, even though the water table does gradually become lowered. The most important feature of the climate, then, is the absence of a really pronounced resting season in spite of the increase of general xerophytic conditions. The textbooks in dealing with this type tend to lay too much emphasis on the summer drought which Warming describes as hostile to vegetation. It certainly leads to an increase in xerophytism, but it is the absence of a complete resting season that explains the retention of the evergreen habit. In

the colder temperate regions evergreen shrubs, e.g. the heathers, are also distributed over regions of relatively mild wet winters.

EVOLUTIONARY TENDENCIES AMONG SCLEROPHYLLOUS TYPES

1. A deep and extensive root-system in proportion to the size of the plants is more or less a universal characteristic. This is to be correlated with the gradual lowering of the water table as summer advances.

2. There is a marked reduction in size of the species. Trees are rare and tall trees do not occur. Yet, though much reduced in size, the majority of the species remain woody even among typically herbaceous families like the Compositae. The dominant shrubs of Macchia reach a height of about twenty feet. Lower-growing heather-like forms appear in the earlier stages of the plant succession.

3. The decreased size is again associated with increased branching. Often the branching is of a dense rigid type.

4. The wood of the species tends to be rather hard and tough.

5. The leaves are sometimes flat and leathery, but in the majority are very much reduced in size and are often of the ericoid type. Heath-like forms belong to a number of widely separated families, e.g. Rosaceae, Leguminosae, Grubbiaceae, Santalaceae, Penaeaceae, Euphorbiaceae, Polygalaceae, Rutaceae, Empetraceae, Bruniaceae, Thymelaeaceae, Verbenaceae, Labiate, Compositae, Epacridaceae, Ericaceae and others.

The marked reduction in size of the leaves is to be correlated probably chiefly with the retention of their evergreen habit. The species have to withstand long periods of adverse conditions due to dryness or low temperatures. Attention has been directed to the ericoid forms chiefly as represented in the cold temperate regions by such types as *Calluna*. The ericoid type is much more richly represented on the mountains and warm temperate regions of Africa where much older phylogenetic forms occur. The Ericads of north temperate regions are a few outlying derivative forms. Physiological explanations should pay more attention to the previous phylogenetic history of plant forms. Yet Schimper's idea of the "physiological drought" supposed to exist under peaty conditions is supported by many. Clements has shown that the peaty soils of moorlands are deficient in aeration, and are thus unsuitable for the development of normal root systems, a factor no doubt of importance as far as plants like *Calluna* are concerned, but it does not apply to the hundreds of ericoid forms at the Cape which have very deep roots. Priestley (1924)

finds that moorland peaty plants form usually large quantities of fats in their roots and from such fatty substances abnormally thick cuticles are formed in the shoots and leaves as well as abnormally early secondary endodermis, cork, etc. He thinks that the early formation of a thick cuticle, etc. may profoundly modify the forms of leaves, and the structure of the shoot generally. All this may be true, but the great majority of ericoid forms do not occur on peat. F. C. Gates (1914) laid emphasis on the necessity for keeping the transpiration within the limits of absorption during winter as the factor explaining xerophily in ericoid forms. Water loss in winter is low, but in evergreen forms it continues to take place even when the water is frozen round the stem and roots. Work of this kind is very useful as showing how ericoid forms have been able to take possession of the habitats they occupy in north-temperate regions, but it does not, of course, explain how the form has been produced. Nor are any attempted correlations between peaty or moorland conditions and the ericoid habit ever likely to explain things fully, since the ericoid form is almost certainly far more ancient than northern peat moors. The whole problem could best be studied at the Cape, where such a multitude of ericads are found belonging to very diverse circles of affinity. It would be very interesting to know how many of the ericoid forms in the separate families mentioned above show the same type of metabolism leading to an accumulation of fats as described by Professor Priestley.

6. Compound leaves are rare among sclerophyllous types in contrast to the drier subtropical vegetation.

7. Lignification. As the name "sclerophyllous" implies, lignification in the leaves is greatly increased. The significance of this has already been discussed. It is much more common in this class of forms than among the drier subtropical types.

8. The bark of sclerophyllous trees and shrubs is well developed.

9. Bud protection by means of bud scales is not prominent; in fact bud scales are rare. This, as in their evergreen habit, is a feature in which sclerophyllous forms come nearer to the primitive evergreen tropical species.

10. Spinosity is also rare, though the margins or apices of the leaves are often prickly.

11. The osmotic pressures of the cell-sap are high.

12. Succulence is very rare.

13. Ethereal oils are a feature of quite a large number of sclerophyllous forms, especially the Rutaceae and the Labiateae. Dixon's

experiments have shown that ethereal oils tend to retard water loss.

14. Minor xerophytic features are common. Thick cuticles are more or less universal, hairy or woolly coverings to the leaves are very common, as are sunk stomata, etc. The leaves are often placed so as not to expose their broadest surfaces to the sun. Many of the leaves are bluish in colour. Schimper, who is followed by Warming, states that the intercellular space systems of the leaves are poorly developed, but our experiments on Natal species by injection methods have shown that mere examination of sections is not to be trusted in arriving at conclusions on this subject.

TEMPERATE WOODY TYPES

The characters of the temperate vegetation are influenced chiefly by the low winter temperatures which lead to a resting period similar to that of the drier subtropical regions. If the winters are dry as well as cold, the winter rest is emphasised, and in the great open Steppe regions woody plants are very rare or absent, the vegetation consisting of grasses and associated herbaceous forms. A winter covering of snow serves as a protection to plants, and the vegetation of regions with winter precipitation does not show such extreme response to the resting season. Evergreen shrubs are able to survive. If the winters are relatively mild and wet without much snowfall, evergreen shrubs may be dominant as in the case of heathers in moorland regions.

In the temperate regions of eastern Asia and Japan, where the record has not been interfered with by the Great Ice period, as has happened so comparatively recently in Europe, the transitions from tropical to temperate are gradual, and in North America where the land connections with the tropics are more open the same statement, to a less extent, applies. The temperate deciduous trees connect with the drier subtropical types rather than with the sclerophyllous types. The reactions to low temperatures are very similar to the reactions to dry winters. The seasonal growth rhythms, however, are more pronounced in temperate trees than in the subtropical. The deciduous habit, in consequence, has become more definitely fixed. The reserve substances often undergo changes during the resting season. As winter approaches, the abundant starch is converted into fats or sugars. Starch is reformed in spring prior to being redissolved and used in the formation of new growth. The growth rate of temperate

trees is increased in summer by the longer daylight, a fact which tends to emphasise still more the seasonal contrast.

EVOLUTIONARY TENDENCIES AMONG TEMPERATE TREES AND SHRUBS

1. The temperate trees and shrubs are very few in number as compared with tropical and subtropical. The temperate woody genera are much smaller than those of tropical and subtropical regions (e.g. *Eugenia*, *Eucalyptus*) or even warm temperate sclerophyllous genera (e.g. *Erica* and *Rhododendron*). Their small numbers and the few species in the genera may be correlated with their relatively short evolutionary history. Such fossil representatives of the same genera as do go rather far back were nearer to the warm temperate and evergreen than the cold temperate and deciduous.

2. Like the subtropical forms they show reduction in height and have stout trunks with increased branching. Their woods are softer than the tropical, though they are usually strong and tough with the mechanical elements well developed. They are harder than many of the derivative subtropical forms. The resistance to winds is more important in the temperate regions.

3. Their leaves are more distinctly modified in response to the fixed deciduous habit. They are thinner, more translucent, more membranous, with usually straighter veins. Preparation for leaf-fall by means of an absciss layer takes place at a relatively early stage in their life. They are built to be used for a short time and then discarded. Their autumn colourings provide a scene never to be observed in the tropics. A very high percentage of them have toothed margins as compared with the trees of tropical forests. They are somewhat smaller in size than the average of tropical forms but marked reduction in size is not a feature of deciduous leaves.

4. Unlike the warm temperate evergreen species and many of the tropical and subtropical, increased lignification is not a feature of the leaves of temperate trees. This is to be correlated again with their fixed deciduous habit.

5. Compound leaves are commoner than among the purely tropical or evergreen warm temperate, but not so common as among the drier subtropical types.

6. Bud protection by means of bud scales is very pronounced.

7. The bark of temperate trees is fairly well developed.

8. Spinosity is rare in contrast with the drier subtropical trees and shrubs.

9. Succulence is not a feature of temperate woody types.

10. Evergreen trees are rare in cold temperate regions and such as do occur are confined to the more favourable situations. Evergreen shrubs are common in the regions of relatively mild wet winters. All this class of cold temperate evergreens are here regarded as derivative from the warm temperate woody vegetation whereas the deciduous cold temperate trees are considered to be more nearly allied to the subtropical forms of dry winter regions.

In conclusion, however, it may be repeated that while it has been found convenient to separate the responses to dry subtropical conditions, to warm temperate conditions with wet winters and dry summers, and to cold temperate conditions, these responses have much in common and are not fundamentally different from one another. They all depend on various slow changes in the basic physiological processes followed by structural changes which have taken place in the course of the evolutionary history of the Angiospermous tree form. Climatic differentiation has led to a certain amount of sorting out of the increasingly diversified forms, but the beginnings of most of the changes can be seen under the relatively constant and very ancient moist-tropical conditions.

SUMMARY

1. In this chapter an attempt is made to trace some of the main ecological evolutionary tendencies among Angiospermous trees and shrubs. The moist-tropical tree type is the most primitive, but during the long period of relatively uniform favourable conditions under the influence chiefly of the biota but, to a much less extent, also, doubtless, through minor changes in the inorganic environment, a considerable amount of differentiation has taken place, as is shown by the list of families to which such forms belong. The contrast between vegetative life and reproductive is not well-marked; their flowers are usually inconspicuous and are produced irregularly at varying seasons of the year; capsular fruits and wind dispersal of seeds are very rare; their seeds are probably not usually very viable. Their woods are generally hard with little storage parenchyma; their trunks are tall and slender, usually supported at the base by buttresses of one kind or another; they are not much branched. Their bark is very thin; thorn development is very rare; their buds are of the "naked" type. Their leaves are usually large, simple, smooth-margined, somewhat leathery and evergreen.

2. Under drier and colder conditions the effects of the inorganic

environment become more marked while the biota has less influence. Emphasis is laid on the fact that physiological changes probably preceded structural changes.

3. Derivative types of trees and shrubs all tend to show to a greater or less extent such features as the following (a) a greater localisation of the reproductive processes both in time and space, (b) the production of softer types of wood, (c) a general reduction in height though not necessarily in the diameters of their stems, (d) an increase of branching, (e) a decrease in size of their leaves, (f) increased bud protection, (g) thicker bark, (i) an increase of minor xerophytic features.

4. Other responses, however, differ according to the nature of the climatic changes. In subtropical regions with dry seasons, with increasing aridity the deciduous habit is adopted or, if the leaves remain evergreen, they are much reduced in size. Lignification in the assimilating organs is often increased. Under semi-desert or desert conditions thorn development is abundant. There is a marked increase in the number of compound-leaved forms. Succulence is a feature of many forms. Increased osmotic pressure in the cell sap is common.

5. In regions with wet winters but dry summers the species remain evergreen but reduction in size goes further. Trees are rare and sclerophyllous shrubs are dominant. They have very deep root systems. Their leaves are much reduced in size and, in a great many widely separated circles of affinity, ericoid forms have been produced. Lignification in the assimilating organs is still more pronounced, but features such as spinosity and succulence are rare. A large number produce ethereal oils and minor xerophytic features are common.

6. Cold temperate trees and shrubs are mostly deciduous and connect with the drier subtropical; a few (mostly shrubs) are evergreen and connect with the sclerophyllous vegetation of regions of dry summers.

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CHAPTER V

DERIVATIVE TYPES PRODUCED UNDER MOIST
FAVOURABLE CONDITIONS

It has already been pointed out that Raunkiaer's system of classifying the life-forms of plants does not lay sufficient stress on the influence of the biota. It has also been shown that, under moist warm conditions, this has been of paramount importance in bringing about differentiation among the most primitive type of Angiosperm. The trees themselves show its effects. They are not all of equal importance from the standpoint of dominance. In moist tropical forest they tend to form several canopies, and those of the lower canopies are, to some extent, dependent on those of the upper canopy. It is unfortunate that we know so little regarding the development of, or plant succession in, tropical rain-forest. The absence of anything approaching pure dominance of single species is, of course, well known, but the exact successional relationships of the extraordinarily mixed assemblage of trees has never been analysed, or at least not in sufficient detail to be of much assistance from our present standpoint.

In dealing with the more distinctly modified types of plant form, however, our task is simpler, and the more important of these will now be dealt with, in each case somewhat briefly.

Lianes. The term liane, at one time applied only to woody climbers, is now generally used for the whole group of climbing plants. H. Schenck is quoted by Schimper as giving an estimate, which probably errs in being too low, that over 90 per cent. of all lianes are tropical. Woody lianes are very rare outside the tropics, the extra-tropical climbers being mostly herbaceous or thin-stemmed derivative types. From the physiological standpoint, lianes differ markedly from the trees over which they climb, in their semi-dependent mode of life. The correlations between this and their morphological modifications are fairly obvious. The internal structure of their relatively thin stems provides for as efficient conduction as possible, combined with strength. Their undulating method of growth, together with such special modifications as hooks, spines, prickles and tendrils of various kinds, prevent their slipping downwards.

Their relationships to the light factor are most important. Often their juvenile stages of growth differ markedly, particularly in their leaf-forms, from the adult stages of their development after they have overtopped the trees and reached full sunlight.

Their study is full of ecological interest from many different standpoints. Their effects on the forest, as a whole, are most marked. They tend to stifle all other forest plants by their abundance and rank growth and shading effects. Since they do not require to use the material they form to build up stout stems, as a support for their foliage, they possess an enormous advantage from the standpoint of economy of effort. In themselves they represent one of the most interesting directions in which evolutionary differentiation has progressed. But, further, they react on the other types, and particularly on the trees over which they grow. They weaken the trees and, assisted by fungal or other parasites, hasten their death. With the death and collapse of the trees open gaps are formed and a renewed struggle for the space left vacant is initiated among the seedlings of the various species present. Thus the process of differentiation in the forest vegetation as a whole is accelerated. The process illustrates very well the "action, reaction and interaction"—to use Osborn's phraseology—of the various evolutionary forces and it demonstrates particularly the outstanding importance of the organic environment under conditions where the inorganic factors are relatively uniform and favourable.

Lianes belong to a large number of diverse families, including the Moraceae (*Ficus*), Aristolochiaceae, Piperaceae (*Piper*), Menispermaceae, Magnoliaceae, Anonaceae, Pittosporaceae, Cunoniaceae, Connaraceae, Leguminosae, Malpighiaceae, Trigoniaceae, Polygalaceae (*Securidaca*), Dichapetalaceae, Euphorbiaceae, Sapindaceae, Hippocrateaceae, Icacinaceae, Sabiaceae, Rhamnaceae, Vitaceae, Dilleniaceae, Marcgraviaceae, Passifloraceae, Ancistrocladaceae, Combretaceae, Araliaceae, Apocynaceae, Asclepiadaceae, Convolvulaceae, Bignoniaceae, Acanthaceae, Cucurbitaceae, Compositae, Palmae (*Bambuseae*), Gramineae, Cyclanthaceae, Pandanaceae, Araceae, Liliaceae, Dioscoreaceae, Orchidaceae (*Vanilla*).

This long list shows clearly that lianes have been produced all through the long history of Angiosperm differentiation. The climbing habit in itself, of course, is much older than the Angiosperms, and there is no reason why many lianes should not have appeared very early among the flowering plants.

THE ECOLOGICAL EVOLUTION OF CLIMBING PLANTS

The classification of climbing plants, usually adopted in the textbooks, is made to depend too much on the modification of various organs which assist in climbing. It is doubtful whether this has more than a very general significance. Among lianes, as among other plant forms, the evolutionary trend has been from the woody to the herbaceous and from the hygrophilous or mesophytic towards the xerophytic. The following classes are arranged in a rough evolutionary sequence.

1. Woody scramblers. This large class of tropical lianes are particularly interesting because so many of them are sufficiently plastic to show very well the origination of the climbing habit. One of the best examples is the South African species *Scutia commersoni* (*S. indica*). In the absence of support it grows often as a rather stout-stemmed tree, sometimes it is a much branched erect shrub, but usually, when it gets an opportunity, it becomes one of the loftiest lianes or "monkey ropes" of the forest. Species of *Dalbergia* and many others behave more or less in the same way. Examples may be found of individuals which begin life, and continue for many years growing erect, and self-supporting, and afterwards produce climbing branches which overtop the neighbouring trees.

2. Woody lianes, in which the climbing habit has become fixed, show more definite modifications. Their stems are thin and often wavy and organs are frequently modified to assist in climbing. "Watchespring" tendrils are common.

3. Mesophytic half-woody or perennial herbaceous lianes. This class is of a distinctly more advanced type and is also more heterogeneous. It may be subdivided according to the methods of climbing that have been adopted, though it is difficult to decide which of those are to be reckoned relatively primitive. Probably they represent diverging lines of ecological differentiation. (a) Root climbers have horizontal anchoring roots often very tough and fibrous, as well as positively geotropic absorbing roots with well-developed conducting elements. (b) Twiners are on the whole more characteristic of open situations or of temperate regions and probably represent a fairly advanced type. (c) Tendril climbers have various organs modified. The degree of modification, of course, gives some indication among allied species as to relative advance but not much stress is here laid on such somewhat superficial phenomena. Even many of the woody lianes have their branches or other organs modified to assist in climbing.

4. Herbaceous geophytic lianes. This class combines underground storage with the climbing habit. The aerial climbing stems are often annual. The *Dioscoreaceae* are the best examples. They are characteristic of regions where the vegetation shows response to a resting season.

5. Xerophytic lianes. In the drier subtropical regions, where succulent and thorny scrub is the dominant type of vegetation, many xerophytic lianes occur. The family of the *Asclepiadaceae* contains numerous examples, but others occur in a variety of other families, e.g. *Euphorbiaceae*, *Vitaceae*, *Cucurbitaceae*, *Compositae* (*Senecio*), *Liliaceae* (*Asparagus*), etc. Many are succulent, others have reduced leaves, etc.

6. Therophytic (annual) lianes. These are all herbaceous and though some, e.g. among the *Cucurbitaceae*, reach surprisingly large dimensions yet the majority are small forms. As in the case of all annual herbaceous types they represent a modern development.

7. Transitions to herbaceous non-climbing types. Around the margins of forests, in grassland areas, on sand-dunes, in waste places, cultivated land, etc., there are many prostrate creeping plants which connect fairly clearly with climbing forms. In families like the *Cucurbitaceae*, *Passifloraceae*, *Convolvulaceae*, where the vast majority of the species are climbers, the origin of the few straggling creeping types is fairly obvious. It can be studied also in certain large genera, such as *Thunbergia* (*Acanthaceae*), *Cissus* (*Vitaceae*), *Ipomoea* (*Convolvulaceae*), etc. While the evidence is entirely insufficient to allow us to argue that all creeping forms originated in this way, there is little doubt that the climbing form, in many cases, represents an intermediate stage in the evolution of the terrestrial herb from woody ancestral forms. It may here be remarked that, from their studies of comparative anatomy, Jeffrey and his pupils, e.g. Eames (1911), as well as Sinnott and Bailey (1914), are apparently of the same opinion, though the latter authors differ from Jeffrey in the details of their interpretation.

Epiphytes. The extraordinary abundance of epiphytes in tropical rain-forest is noted by all explorers of such regions, but they hardly occur outside the tropics, and moist subtropics. They represent a specialised class of derivative forms which have responded to the effects of the organic environment. Schimper (1903) has classified them into (a) Proto-epiphytes, (b) Hemi-epiphytes, (c) Nest Epiphytes and (d) Tank Epiphytes, but this classification once more does not follow quite a proper evolutionary sequence, though these different

classes do form fairly natural ecological groups. The following arrangement follows a slightly more natural order from the standpoint of ecological evolution.

1. The so-called "pseudo-epiphytes" connect very closely with the lianes. They begin their life as climbers and later on become epiphytic by their stems dying off from below upwards.

2. On the other hand, various species of *Ficus*, *Clusia*, *Carlu-dovica*, *Philodendron*, *Anthurium*, etc., reverse this process. At first they are epiphytic, but later they send absorbing roots down into the soil, and they may become independent. When such epiphytes become established in the soil they are practically lianes. Only some of them ultimately kill their supporting host, and remain entirely independent, and of these the banyan figs are the most important, indeed several of them are among the largest, if not the very largest, of all plants. This class is Schimper's "Hemi-epiphytes." They again show the close connection with the climbing habit, but they represent a more advanced type than the pseudo-epiphytes.

3. Proto-epiphytes are forms which obtain their water and food supply from the surface of the supporting structure. They are often xerophytic, often have provision for water storage, as in the pseudo-bulbs of the epiphytic orchids, sometimes their roots do not differ from terrestrial forms, in other cases they possess velamen. This class includes the majority of the not too highly specialised epiphytes, and it is important to note that many of them occur on rocks or other similar situations where competition from other plants is not too severe or they can be cultivated in soil.

4. Nest Epiphytes. These collect soil and humus in various ways by means of interwoven roots or by "pocket leaves."

5. Tank Epiphytes. These have roots developed only as anchoring organs, or their roots are entirely suppressed so that nutrition is supplied only by the leaves. The Bromeliaceae are the only representatives of this class. They absorb water by means of the peltate scale-hairs situated on their leaf bases. *Tillandsia usneoides* is the most highly specialised of all. When mature, it consists only of thread-like shoots covered with scale-hairs.

6. A few terrestrial herbs appear to connect with and may have been derived from epiphytes. Among the Bromeliaceae, the terrestrial cultivated pineapple is floristically an advanced type. That velamen is not confined to the aerial roots of epiphytic orchids and aroids but occurs on the roots of many terrestrial species as well, has been shown by the work of Goebel (1922), of Moss (1924) and others (cf. Mrs Arber,

1925, p. 16). Not only is velamen found on the roots of a variety of terrestrial orchids, but in forms like *Crinum longifolium*, *Crinum powellii*, *Aspidistra elatior*, *Clivia nobilis*, *Agapanthus umbellatus*. Many of these are forest margin types, others spread through grassland areas. We have mentioned the fact that many epiphytes are capable of growing in soil and if in general they have, as a group, been evolved from the lianes it seems natural to suppose that they may have given rise to terrestrial forms and not, as is generally assumed, have originated therefrom.

THE ORIGIN AND GENERAL DIFFERENTIATION OF SUFFRUTICOSE AND HERBACEOUS TYPES

Various references have already been made to the different ways in which suffruticose and herbaceous Angiosperms have originated. We have seen that, while certain families may be entirely or predominantly woody, nearly allied but more advanced families may be herbaceous (e.g. Araliaceae and Umbelliferae, Myrsinaceae and Primulaceae) or certain tribes in well defined families may be relatively primitive and woody, other tribes more advanced and herbaceous (e.g. Ehretioideae and Cordioideae as compared with the Borraginoideae among the Boraginaceae). We have seen also that the herbaceous habit may arise within very narrow circles of affinity as in certain large genera, e.g. *Hibiscus*, *Solanum*, *Euphorbia*. Burtt-Davy (1922) has dealt with examples of intermediate suffruticose forms arising in several distinct woody genera, e.g. *Acacia*, *Eugenia*, *Elephantorrhiza*, *Parinarium*, *Erythrina*, *Menodora*, *Clerodendron* and *Zizyphus*. The work of Jeffrey and Sinnott and Bailey already quoted gives much comparative anatomical information regarding the course of the changes involved. To enter into a discussion regarding their separate viewpoints, and the differences between them, would take us too far (but see Jeffrey, 1917, Jeffrey and Torrey, 1921, Sinnott and Bailey, 1914, 1922). They agree that the herbaceous type among Angiosperms is derivative, a view which Sinnott and Bailey state was apparently first put forward by Hallier (1905).

It is now desirable to examine the possible lines along which the modern herbaceous forms may have been produced. Under the influence of the biota in moist tropical regions one line of evolution apparently has been from trees to woody lianes, then to herbaceous lianes, then to straggling types and finally to herbs. Another possible line has been from trees to lianes as before, then to epiphytes

and then to herbs. But we cannot suppose that these two methods of origin exhaust the possibilities. The mass of evidence from phylogeny brought together in previous articles would appear to indicate that by continued reduction in size, trees gave rise to shrubs, then to undershrubs and these in turn to herbs. There are a multitude of intermediate suffruticose forms which are woody underground or at the base and bear herbaceous aerial branches, but, as already mentioned, these may arise within single large and predominantly woody genera. In the direct passage from tree to shrub, undershrub and herb, however, as a rule the inorganic factors of the environment have played a part—probably a more important part than the biota. Large groups of Angiospermous herbs probably owe their origin to the lowering of temperatures, others to increasing aridity. The numerous and highly differentiated types of herb found in drier and colder regions will be dealt with later. At present we shall confine our attention to the relatively primitive types occurring as undergrowth in the forest as forest margin plants, and as marsh and stream-bank plants (*helophytes*). All these habitat types have much in common. They are, to a large extent, independent of climatic differentiation, though, of course, climate does have some effect in controlling their distribution and in the course of time it has also led to some degree of differentiation among them. It should also be remembered that the habitat is of an ancient primitive unchanging type and the great lapse of time has led to differentiation.

FOREST UNDERGROWTH, FOREST MARGIN, MARSH AND STREAMBANK TYPES

From the physiological standpoint the most important factors influencing this group are summed up in the term "hygrophilous." The supply of water to their roots is, as a rule, sufficient for all their needs. They may occasionally have to withstand periods of relatively adverse conditions and, just as the dominant trees in tropical forest, because of their inefficiency in water conduction may suffer during brief intervals of drought and, therefore, show some xerophytic characters, such as leathery leaves, so also, many *helophytes*, particularly in colder and drier regions, may be somewhat xerophytic or, as many writers prefer to express it, "xeromorphic." The xerophytic appearance of many sedges and rushes, etc., has been variously explained as due to "physiological drought," to lack of aeration in the substratum, to accumulation of acids in bogs and swamps and generally by supposing that the process of absorption, even when the

water supply is plentiful, may be interfered with. It is well to remember, however, that in the subtropical regions with dry seasons the water supply, even in marshy places and around forest margins, is not always plentiful. There are intervals of more or less unfavourable conditions. In cold temperate regions absorption is drastically interfered with by the lowering of temperatures in winter when the water may be frozen. It is under such conditions of occasional adversity that xeromorphic helophytes occur. If they are found under conditions that are continually and uniformly favourable, they must be very rare. They hardly occur, for instance, as forest undergrowth in moist tropical regions. If there are exceptions to this rule it should be remembered that their previous phylogenetic history must be taken into account. The epiphytes of tropical rain-forest, as we have seen, usually are more or less xerophytic.

Lack of aeration in the substratum is, of course, often a factor of importance. Correlated with it is the prevalent high development of the intercellular aeration system in helophytes. The substratum is often unstable and plants with underground creeping rhizomes are then predominant. Apart from this, however, owing to the prevailing uniformity of conditions, provision for underground storage is not particularly prominent. Only in colder and drier regions are true geophytes abundant. The creeping underground rhizomes of marsh and forest margin plants bear adventitious roots which help to fix the plants firmly and the plants themselves in turn help to fix the soil. Where growth is continuous food is only stored temporarily and new leaves are continuously produced. This creeping habit of growth is quite unlike the erect habit of woody trees and shrubs but, as we have seen, it is not far removed from the creeping habits of many prostrate forms closely allied to lianes. The light factor is important chiefly among the forest undergrowth types, which connect fairly closely with the more light-demanding forest margin and marsh forms. Probably most shade-loving plants are to be considered rather highly evolved. As a rule they show floristic advance as compared with the more light-demanding types, though some that connect, perhaps directly, with climbing types are more primitive, e.g. among the Araceae.

SYSTEMATIC COMPOSITION AND DIFFERENTIATION

It is impossible to mention all the orders or families which contain plants belonging to this class but the following are the most important: Pandanales, Helobiaeae, Palmae, Araceae, Gramineae, Cyperaceae,

Eriocaulaceae, Restionaceae, Juncaceae, Commelinaceae, Scitamineae, Orchidaceae, Piperaceae, Ranunculaceae, Rosaceae, Leguminosae, Euphorbiaceae, Malvaceae, Geraniaceae, Begoniaceae, Melastomaceae, Lythraceae, Onagraceae, Halorrhagaceae, Umbelliferae, Labiate, Scrophulariaceae, Acanthaceae, Gentianaceae, Boraginaceae, Rubiaceae, Valerianaceae, Dipsaceae, Compositae.

The most striking fact is the abundance and dominance of the Monocotyledons. Many of the Dicotyledons are weak stragglers, others are small creeping forms, and there are many suffruticose forms. There are, of course, also many woody shrubs along the forest margins but these have been dealt with already. The woody types become more prominent as the succession advances, and the derivative herbaceous types are ousted, the stages of succession, as already explained, more or less reversing the order of evolutionary development.

The Monocotyledons of this class demand closer attention from the evolutionary standpoint. In all parts of the world to-day where moist situations are not dominated by woody Dicotyledons, they are by Monocotyledons, usually either by grasses or sedges. Theories regarding the actual origin of the Monocotyledons are still too uncertain to allow of much reliance being placed on them, but for those who follow Engler's system of arrangement it is interesting to find that the relatively primitive families more or less all belong to this class, whether we consider the group as a whole or special circles of affinity. In the first case, the Typhaceae, Sparganiaceae, Pandanaceae, Helobiaeae, many Palms and most of the Araceae are all hygrophilous (or aquatic) or forest margin forms, while in the second case the Eriocaulaceae among the Farinosae and Juncaceae among the Liliiflorae are of the same class.

Both the Pandanaceae and Araceae are particularly interesting since they include climbing forms (and the latter epiphytes as well).

Several of the primitive hygrophilous Monocotyledons are woody, but whether this is significant or not is rather uncertain. The general appearance and form of the arborescent species of *Pandanus* (screw pine) with relatively thin stems supported by stilt roots is similar to dicotyledonous rain-forest woody plants, though the internal organisation is so different. The palms, though many modern representatives are xerophytic, probably had, like the screw pines, an hygrophilous origin. They occur as undergrowth in tropical rain-forest and some of them, e.g. *Nipa fruticans*, are dominant swamp plants lining the landward side of mangrove areas. Other examples

are *Bactris* sp., *Elaeis guineensis* and *Phoenix paludosa*. There are also woody forms among the great dominating families Juncaceae (*Prionium*), Cyperaceae (*Schoenodendron*) and Gramineae (*Bambuseae*). The fact that the bamboos are floristically primitive is interesting, but since the woody habit among Monocotyledons is built up on such distinct lines from the Dicotyledons, in itself it is not generally regarded as necessarily primitive. The woody habit also occurs in types like *Dracaena*, *Yucca* and *Aloe*, which show advanced responses to dry conditions.

We have already noted the fact that the forest margin and marsh types tend to become very widespread. This is largely due to the uniformity and ancient unchanging character of the habitat, though, doubtless, in the actual dispersal of the species the birds that feed in marshy places and along stream banks have played an important part. The ancient tropical forms tend to give rise to isolated species which spread far into temperate regions. This is well seen in the Araceae, where so many evolutionary stages are illustrated. Not only are climbing forms and epiphytes, as well as herbs of the under-growth, prominent in tropical forest but many marsh forms are widespread in the warmer regions, while types like *Calla* and *Acorus* occur in north temperate regions reaching even to the subarctic zone.

The differentiation of such a typically marsh family as the Cyperaceae is also worthy of detailed and careful study. The separate tribes are, on the whole, sufficiently well-defined. In the tribe Scirpeae the large genus *Cyperus* and its allies are relatively primitive, and are dominant in the tropical regions. More reduced or modified derivative genera like *Heleocharis* and *Scirpus* have spread widely outside the tropics, while the cotton-grass *Eriophorum* is a north temperate or arctic genus. The smaller tribes, Hypolytreae, Rhynchosporeae, Hoppieae and Sclerieae, are, for the most part, found in the warmer parts of the world, and, since they include forms which have the remnants of a perianth, they are, in at least some respects, fairly primitive floristically. Schönland (1922) finds that the general liliaceous floral diagram is fully realised in the South African genera, *Macrochaetum* and *Tetraria*, which have a mountainous south-western distribution—a region where so many very ancient warm temperate types are found, as explained in previous chapters. In the relatively advanced tribe, the Cariceae, the primitive genus *Schoenoxiphium*, which appears to be near the ancestral form of the genus *Carex*, is another African species occurring often around forest margins as well as in marshy places. The huge genus *Carex*, on the other hand,

with about 800 species, has spread all over the temperate, alpine and arctic regions of the world. More intensive work is admittedly required, but so far as a superficial examination permits us to judge, it would appear that all through this great family the evidence from phylogeny lends strong support to the views which we have set forth regarding the origin, differentiation and spread of the hygrophilous herbaceous form. The beginnings are seen under favourable conditions around forest margins, spread takes place through marshes and along stream banks, early responses to temperate conditions are shown on the mountain ranges of the tropics, and particularly on the very ancient mountain ranges of Africa, and the colder temperate regions are occupied by the most highly modified types such as the genus *Carex*.

As was pointed out very briefly in our systematic account the Eriocaulaceae and Restionaceae and allied families, taken together, show exactly the same general course of differentiation. While their origins can be traced back to the forest margins and marshes of the tropics early response to temperate conditions (as in the case of the Restionaceae) are shown on mountain ranges in the south-western region of South Africa and in Australia.

The Juncaceae are important as representing primitive members of the Liliiflorae, considered by some to be allied to the palms. They are hygrophilous but not markedly geophytic. While tropical forms are common enough, and the solitary woody genus *Prionium* is subtropical, on the whole the Juncaceae are mountainous or temperate and, as is to be expected from this distribution, show several features of relative advance. Their xeromorphism has already been discussed. It is only fair to add that all authorities are not agreed that they are to be considered the most primitive members of the Liliiflorae.

The general evolutionary advances reached by this class of derivative plant forms may now best be summarised by giving their main characteristics, structural features and behaviour as follows:

1. The dominant species are nearly always Monocotyledons (grasses, sedges, Restionaceae, Juncaceae, *Typha*, etc.).
2. The majority are perennials, but where a very pronounced dry season leads to a drying up of the water in the substratum, annual species are present.
3. The majority have mesophytic leaves yet some are xeromorphic. The latter, however, are more or less confined to regions where dry or cold seasons occur.
4. Underground creeping rhizomes with adventitious roots fix

the dominant plants firmly in the shifting soil and cause dense social growth producing pure associates.

5. Tufted forms also occur. The tufts tend to be gradually lifted up on their own dead remains and become spongy masses, which lift the water by capillarity—a relatively advanced type of plant form seen for the most part in temperate regions, e.g. *Eriophorum*, *Carex* spp.

6. Among the Monocotyledons the aerial stems are usually unbranched and end in inflorescences.

7. The Dicotyledons are more sparsely scattered, very seldom dominant and are usually weak stemmed, erect or often straggling or creeping forms.

8. When there is a lack of good aeration in the substratum, helophytic species have usually a well-developed aeration system.

PARASITES, SAPROPHYTES AND INSECTIVOROUS PLANTS

The general morphology of these specialised types is very fully dealt with in systematic works, and the larger general text-books of botany, so they may be considered very briefly here. In tropical forest parasites belong for the most part to specialised small families, e.g. Loranthaceae, Balanophoraceae, Rafflesiaceae, and are often very highly modified forms. Hemiparasites on roots are more abundant outside forest areas, in drier, more open types of plant formation or in temperate regions. Their general systematic relationships have already been dealt with. Genera and even species of parasites in many cases tend to become extraordinarily widespread, a fact which is, in some ways rather surprising, considering their highly specialised mode of life and obviously derivative character. It may perhaps be correlated with their possessing, as a rule, very light seeds which are easily scattered by the wind, though wind dispersal in the case of other plants does not necessarily lead to very wide distribution. Saprophytes occurring in tropical forest include the Triuridaceae, Burmanniaceae and many Orchids, as well as other genera such as *Voyria* among the Gentianaceae. Outside the forest areas there are members of the Scrophulariaceae and other families. The problem of saprophytism, and particularly hemisaprophytism, is, of course, intimately bound up with the question of the symbiotic union of flowering plants and mycorrhizal fungi.

The insectivorous plants represent another highly specialised type, but they have been sufficiently dealt with in our general systematic survey.

AQUATIC PLANTS

Hydrophytes or aquatic plants among the Angiosperms are probably all rightly regarded as derivative, though they have originated in many widely separated circles of affinity. Among the Dicotyledons the Nymphaeaceae, Ceratophyllaceae, Podostemonaceae, Hydrostachyaceae, Tristichaceae, Callitrichaceae, and Hippuridaceae are entirely aquatic. Aquatic representatives also occur in many other families, e.g. Ranunculaceae, Cruciferae, Droseraceae, Crassulaceae, Portulacaceae, Elatinaceae, Polygonaceae, Lythraceae, Onagraceae, Umbelliferae, Primulaceae, Gentianaceae, Scrophulariaceae, Lentibulariaceae, Plantaginaceae, Rubiaceae, Compositae. The Monocotyledons include a much higher proportion of aquatics. The whole series of families belonging to the Helobiae are, with very few exceptions, entirely aquatic, as are the Lemnaceae and Pontederiaceae, while water-plants also occur among the Cyperaceae, Gramineae and Sparganiaceae.

The physiology and structure of aquatics are well known and need not be discussed in great detail. Water is a denser medium than air and gases reach the submerged aquatics only through solution. Light is diminished in amount with increasing depth. Most of the structural modifications are to be correlated with these simple facts. In fixed rooting aquatics the roots may absorb water or may act only as fixing organs. Water is also absorbed all over the surface of the plant. The epidermis is thin and usually without cuticle. The occurrence of chlorophyll in the epidermis is to be correlated with the diminished light supply. The water-conducting system is reduced in amount and centrally placed. Secondary growth in thickness rarely takes place, there being, as a rule, no functional cambium. Mechanical tissue is rarely present to any extent. The aeration system is always well developed.

Yet, in spite of the fact that water is a wonderfully uniform environment, and the reactions and modifications mentioned are fairly general amongst all aquatics, the really striking thing about the group is the large amount of differentiation shown. This is, of course, to a large extent understandable in view of their exceedingly diverse points of origin. Much may be explained by taking into account previous phylogenetic history. But in considering the differences between the separate species of the larger aquatic genera, and in considering the differentiation of the well-defined and wholly aquatic families, such as the Podostemonaceae, it is not so easy to

understand how the high degree of differentiation has been brought about. The same problem on a much larger scale is presented by the evolution of life in the sea. It is true that many aquatic species appear to be physiologically sensitive to very slight changes in the external medium, and show corresponding structural changes in leaf size, leaf shape, etc., and it may be the case that the water environment is not so very uniform after all, yet when all possible allowance has been made for the influence of external factors, one is forced to the conclusion that, in the case of the aquatics, internal forces are responsible for a large amount of differentiation, and these internal forces are not much modified in their effects or results by any action of the external environment.

The same thing applies, as we have seen, to differentiation under relatively uniform conditions among land plants as in tropical rain-forest and indeed under all other conditions. The internal forces supply the diverse forms on which the external forces act by sorting out forms suited to each habitat. When the external environment, as in the case of water, is a very uniform one and there is not much competition for space (i.e. when the biota is not important) the diverse forms may, under such circumstances, very well persist. The biota, however, in the case of aquatic plants, is often of at least some importance as it is to a much greater extent in tropical rain-forest.

THE GENERAL EVOLUTIONARY HISTORY OF AQUATIC FORMS

Aquatics have not all become equally highly specialised. There are all gradations between forms, which do not differ markedly from land plants and such very highly modified types as the *Lemnaceae*. The classification of aquatic plants adopted by Mrs Arber in her recent work (1920) follows an earlier scheme of Schenck and essentially it represents a rough evolutionary sequence.

- I. Plants rooted in the soil.
 - A. Essentially terrestrial forms that can live in water without marked adaptation (*Achillea ptarmica*, *Cuscuta alba*, *Glechoma hederacea*).
 - B. Essentially terrestrial forms which sometimes produce modified submerged leaves (*Sium latifolium*).
 - C. Plants which produce three types of leaves, submerged, floating and aerial (various *Helobiaeae*, *Ranunculus*, etc.).
 - D. Submerged plants with aerial foliage leaves or aerial inflorescences.
 - E. Entirely submerged plants with hydrophilous pollination.

- F. The highly modified, commonly thalloid, Podostemona-
ceae, Hydrostachyaceae and Tristichaceae.
- 2. Non-rooted Aquatics.
 - A. Floating.
 - B. Entirely or partially submerged.

This scheme of classification represents one of the earliest attempts to arrange any class of plant forms in an evolutionary sequence. Aquatics among flowering plants, as a rule, represent a final and specialised evolutionary stage. Once the aquatic habit has been definitely adopted, as it appears to have been in many cases early in the history of the Angiosperms (especially the Monocotyledons), a subsequent return to land life among forms resulting from further differentiation has rarely taken place.

According to a theory of Scott's (1890), however, the origin of polystely in Dicotyledons is due to such infrequent occurrences. Aquatic plants, as we have mentioned, have generally no functional cambium. A structure once lost, according to Dollo's "Law of Irreversibility," which has been further elaborated for plants by Mrs Arber (1920, p. 181 and p. 336), cannot be regained. If any aquatic returns to terrestrial life it has difficulty in renewing its cambium. Instead of doing so, according to Scott, it meets the increased demand for a vascular-carrying system by multiplying the number of steles. *Gunnera*, *Auricula* and *Pinguicula* are examples of terrestrial plants which may have had aquatic ancestors.

If it be admitted, as it is by most botanists, that the aquatic plant form is derivative, then it must be granted that the above scheme of classification is a perfectly natural one, proceeding as it does from the purely terrestrial to the most completely aquatic types. It is interesting, therefore, to note that, as in the case of the xerosere so also in the hydrosere, the successive evolutionary stages are the reverse of the stages of the plant succession. The usual stages of the plant succession in the hydrosere everywhere are (1) Floating aquatics, (2) Rooting submerged aquatics, (3) Reed grasses, *Typha*, etc., with only their lower parts submerged, (4) Sedges and other marsh plants, (5) Hydrophilous shrubs or herbs, (6) Mesophytic vegetation. The plant succession proceeds from the aquatic to the mesophytic and terrestrial. The evolutionary differentiation of the plants concerned has proceeded in exactly the opposite direction. So that generally both for the stages of the xerosere and the hydrosere, plants appearing relatively early in the plant succession are relatively highly evolved ecologically.

SUMMARY

1. Under moist favourable conditions the effects of the biota are of paramount importance, resulting in the production of various derivative types of plant form, lianes, epiphytes and terrestrial hygrophilous suffrutices and herbs. The latter occur as forest under-growth and forest margin types but tend to spread widely in marshy situations and along stream and river banks. The specialised types of parasites, saprophytes, insectivorous plants and aquatics are also considered.

2. Lianes belong to a large number of diverse families and in their evolutionary history progress from the woody to the herbaceous and from the hygrophilous or mesophytic towards the xerophytic. Woody scrambles which sometimes grow erect, woody lianes of fixed climbing habit, half-woody or herbaceous lianes with organs often modified for climbing, herbaceous geophytic lianes, xerophytic lianes, annual lianes and creeping herbaceous stragglers, which do not grow erect, are different classes arranged somewhat roughly in an evolutionary sequence.

3. Epiphytes connect with lianes the so-called "pseudo-epiphytes" or climbing forms which become epiphytic, forming an intermediate group. Hemi-epiphytes reverse this process. Proto-epiphytes are the class including the orchids, aroids, etc., where the epiphytism is definitely fixed. Nest epiphytes and tank epiphytes are still more specialised. There are a few indications from phylogeny as well as from comparative morphology (the occurrence of velamen on the roots of terrestrial herbs) that epiphytic forms may have sometimes become terrestrial.

4. Herbs of the forest margin, marshes and stream bank may have originated often from climbers or epiphytes, but the herbaceous form in general, with increasing climatic differentiation probably arose frequently by reduction in size of woody plants giving a series, trees, shrubs, undershrubs and herbs. The series is illustrated even with the limits of many large genera. In this class of herbaceous forms the dominant species are usually monocotyledonous, perennial plants with underground rhizomes. The Dicotyledons are usually weak-stemmed, erect or straggling species. Tufted forms also occur. In regions with adverse seasons xeromorphic or annual forms are found.

5. The specialised classes of parasitic saprophytes and insectivorous plants, since they are well known in their general features, are dealt with very briefly.

6. Aquatic plants are classified according to the scheme (originally due to Schenck) adopted by Mrs Arber in her recent book. Progressive stages are shown from land forms to the most highly modified of floating aquatics. The evolutionary series more or less reverses the stages of the (hydrosere) plant succession.

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(To be continued.)

A SUMMARY OF DISCONTINUOUS GENERIC DISTRIBUTION IN THE ANGIOSPERMS

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FEW aspects of plant-geography are of greater interest and importance than that of widely discontinuous distribution. Not only are the facts of discontinuity in themselves very remarkable but a theoretical consideration of them has a direct bearing upon two important problems, the history and phylogeny of the Angiosperms and the evolution of the present land configuration of the globe. Discontinuity, for these reasons, is a subject which interests not only the botanist but also the geologist and geodesist. This is particularly so at the present time, when theories of continental displacement await the verdict of the scientific world, because a study of such distribution is most likely to reveal botanical evidence of value in the discussion. It is therefore common to find examples or supposed examples of discontinuity mentioned in the literature of these theories. Unfortunately the plant-groups selected as examples are often most unsatisfactory and are quoted without any real knowledge of their distribution. Wegener himself, for instance, quotes the genus *Calluna* as presumably affording, by its distribution in eastern North America and Europe, evidence of the gradual separation of these regions. There are quite a number of genera which would have provided really authentic examples of such discontinuity in their natural range but *Calluna* is not one of them, since it is as certain as such things can be that the New World plant is adventive from the Old World. At least the genus is one of the last to be mentioned in this way and its quotation tends to weaken the author's position rather than to strengthen it.

These unsatisfactory citations appear partly because, so far as I am aware, there is no list of widely discontinuously distributed genera or similar groups which is in any way critical. It seemed that this lack might to some extent be remedied by a careful, and as far as possible, critical examination of all the genera which have from time to time been credited with such a range provided that the writer had access to most of the pertinent literature and to many of the actual specimens. From such an examination a list of genera and

similar groups could be compiled which might, with some confidence, be used for reference when questions of discontinuity arise. The work here described was undertaken with this object in view, but to make it of the greatest use its limitations must be clearly understood.

It was manifestly impossible to examine all the genera very minutely or to carry out detailed dissections, and in general I have been content with a careful superficial examination with or without the use of a lens. The basic principle underlying the whole subject of discontinuity is that the only significant examples of such distributions are those in which it is possible to be reasonably satisfied that the plants concerned are truly monophyletic, i.e. have comparatively recently descended from a common ancestor and *ipso facto* have arisen in a common or continuous locality. The fact that similar plants grow in widely separated places loses all immediate theoretical value unless community of origin can be assumed and it was chiefly for this reason that the genus was made the basal unit for work since it is this unit more than any other which has a monophyletic conception behind it. My task thus became that of discovering, among the flowering plants, as many units as possible of about generic size, presumably monophyletic, and having widely discontinuous distributions. It was, of course, necessary to lay down somewhat arbitrarily what should be considered to constitute discontinuity and the term is here used to mean the occurrence of one or more species in two or more parts of the earth's surface separated by areas of land or sea of at least continental dimensions. For the purposes of this search careful superficial examination associated with a study of the literature and, if necessary, some dissection was thought sufficient and any more detailed investigation would probably have vitiated the results by unduly magnifying minute and phylogenetically unimportant differences.

It was soon evident that many often-quoted genera could not be included in the list. This was usually for one or both of two reasons. The first of these is unsound taxonomic conception and the consequent union of unrelated and/or dissimilar forms. Species have frequently been described from inadequate material and included, without valid reason, in certain genera, thereby giving them a discontinuous range. These inaccuracies have sometimes been corrected when completer material became available, but more often their correction has been overlooked and the original statements have persisted unchallenged. Sometimes the genera as usually

accepted are very heterogeneous, consisting of two or more sections or subgenera differing markedly and together making an assemblage of species which cannot possibly be considered as monophyletic. A particular form of this error results from the slavish acceptance of a single character as generically diagnostic. The present tendency of taxonomy is to correct this by increasing the number and decreasing the size of genera but there are still many anomalies. In other cases genera are made to contain all those species which differ from a pre-existing genus in one character, irrespective of their probable origin, which if the first genus is very widespread, may well be polyphyletic.

The second great source of error is a tendency to consider plants as native when they are actually the result of introduction. Sometimes the adventive plant has even been described as a different species (cf. *Calluna*). Misquotations of locality and typographical mistakes have also helped to swell the list of spuriously discontinuous genera.

The greatest practical difficulty was to find the true natural limits of many of the plant-groups. Sometimes it was obvious that geographically two or more taxonomic genera must be considered together (and this has been done in the list); in other cases single genera contained more than one natural group. Where, in the following lists, a genus must be considered in its narrowest sense, or in part only, an asterisk has been placed after the name. Unfortunately many very large plant-groups, even families, are in such a confused and incompletely known condition that they have had to be almost entirely ignored. Their inadequate representation means that until a detailed and extensive revision is undertaken they will not afford distributional data of value.

It is obvious that the following lists of genera are to a large extent merely the results of a personal opinion and are therefore open to criticism by those who hold other views. At the same time one opinion associated with certain definite criteria has been applied to all the genera and they should therefore be of consistent comparative value throughout even if their absolute value cannot be determined. It must be again emphasised that the inclusion of any genus in the list does *not* mean that it has been revised taxonomically but that a careful examination shows that it either forms by itself, or contains within itself, a group of species which has a discontinuous range and which is presumably monophyletic.

It cannot be hoped or claimed that the list is complete and there is apparently no means of ensuring finality short of a complete revision of the whole of the Flowering Plants. It is, however, be-

lied and hoped that the facts here given and the opinions expressed are sufficiently trustworthy to form a basis from which discontinuous distribution can be studied more advantageously than before. Owing to considerations of space and cost only the names of the genera and the authorities for them are given in the following lists but further details of constitution, distribution and literature have been preserved in card-index form. It is hoped that the list may be kept up to date by the publication of supplementary lists at convenient intervals of time. For this purpose the author will welcome data and expressions of opinion from those engaged upon more intensive studies of smaller plant-groups.

The list is divided into five main sections, each of which is further subdivided according to the details of the distributions of the genera included. The term "Madagascar etc." is used to cover any or all of the islands of the Indian Ocean south of the equator and west of 70° E. longitude. The list contains about 700 genera and this number may be taken as of the order of 5 per cent. of all the genera of Angiosperms.

A. GENERA FOUND ENTIRELY OR PREDOMINANTLY
IN THE NORTH TEMPERATE ZONE.

a. Discontinuous over the whole North Temperate Zone.

Aesculus L. and *Hippocastanum* Rupp., *Apocynum* L., *Bifora* Hoffm., *Carpinus* L., *Cercis* L., *Fagus* L.*, *Gleditschia* Clayton, *Hypopitys* Dill., *Liquidambar* L., *Narthecium* Moehr., *Ostrya* Mich., *Paeonia* L., *Philadelphus* L., *Pistacia* L., *Staphylea* L., *Tilia* L.

b. Europe and/or W. Asia and E. Asia.

Bosea L. and *Rodetia* Moq., *Forsythia* Vahl, *Parrotia* C. A. Mey. and *Fothergilla* Murr. p.p., *Pterocarya* Kunth, *Wulffenia* Jacq., *Zelkova* Spach.

c. N. America, Europe and W. Asia.

Ammophila Host., *Arbutus* Adans., *Cakile* Adans., *Cinna* L., *Comandra* Nutt., *Corema* D. Don, *Datisca* L., *Douglasia* Lindl., *Eryngium* L., *Eurotia* Adans., *Heberdenia* Banks, *Littorella* Berg., *Loeflingia* L., *Lupinus* L., *Platanus* L., *Spartina* Schreb.*, *Specularia* A. DC.

d. N. America (especially in the West) and in Central and/or E. Asia.

Boschniakia C. A. Mey., *Boykinia* Raf., *Chamaesaracha* A. Gr., *Clintonia* Raf., *Dicentra* Bernh., *Echinopanax* Decne. et Planch.,

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Enemion Raf., *Mitella* L., *Monotropa* L.*., *Nephrophyllidium* Gilg, *Stenanthium* Kunth, *Thermopsis* R. Br., *Trillium* L.

e. E. N. America and both continental and insular E. Asia.

Amsonia Walt., *Aplos* Moench., *Buckleya* Torr., *Calycanthus* L. and *Chimonanthus* Lindl., *Caulophyllum* L. C. Rich., *Cladrastis* Raf., *Cryptotaenia* DC., *Hamamelis* L., *Houttuynia* Batsch. and *Anemopsis* H. et A., *Kraunhia* Raf. and *Wistaria* Nutt., *Menispermum* L., *Pachysandra* L., *Panax* L., *Penthorum* L., *Phellopterus* Benth., *Phryma* L., *Podophyllum* L., *Saururus* L., *Shortia* T. et G., *Stewartia* L., *Symplocarpus* Salisb., *Tipularia* Nutt., *Triosteum* L., *Xanthoxylum* L.*

f. E. N. America and continental E. Asia only.

Aletris L., *Campsis* Lour., *Chionanthus* L., *Decumaria* L., *Gymnocladus* Lam., *Jeffersonia* Barton, *Liriodendron* L., *Pyrularia* Mx., *Stylophorum* Nutt.

g. E. N. America and Japan only.

Achlys DC., *Arethusa* L., *Chiogenes* Salisb., *Croomia* Torr., *Diarrhena* Beauv., *Diphylleia* L. C. Rich., *Epigaea* L., *Hydrastis* Ellis and *Glaucidium* S. et Z., *Mitchella* L., *Trautvetteria* Fisch. et Mey.

h. E. N. America and E. Asia, with extensions into the tropics of one or both hemispheres.

Abelia R. Br., *Aralia* L., *Astilbe* Buch.-Ham., *Berchemia* Neck., *Catalpa* Scop., *Disporum* Salisb., *Gelsemium* Juss., *Gordonia* Ellis, *Halenia* Borkh., *Halimium* Willk., *Hydrangea* L., *Illicium* L., *Itea* L., *Ligustrum* L., *Magnolia* L., *Nelumbo* Adans., *Nyssa* L., *Photinia* Lindl.*., *Schizandra* L. C. Rich., *Talauma* Juss.

B. GENERA FOUND ENTIRELY OR PREDOMINANTLY IN THE TROPICAL REGIONS, BUT EXCLUDING PAN-TROPICAL GENERA.

a. America, Africa and/or Madagascar etc.

i. America, Africa and Madagascar etc.

Astephanus R. Br., *Bertiera* Aubl., *Buxus* L., *Caperonia* St. Hil., *Carpodiptera* Griseb., *Cassipourea* Aubl. and *Weihea* Spreng., *Eichhornia* Kunth, *Elaeis* Jacq., *Eulophidium* Pfitz., *Hirtella* L., *Landolphia* Beauv., *Melinis* Beauv., *Mohlana* Mart., *Mostuea* Didr. and *Leptocladus* Oliv., *Paullinia* L., *Pentodon* Hochst., *Piriqueta* Aubl., *Raphia* Beauv., *Sabicea* Aubl., *Savia* Willd., *Sympiphonia* L., *Trachypogon* Nees, *Trichilia* L., *Vellozia* Vand., and *Barbacenia* Vand.

2. America and continental Africa only.

Amanoa Aubl., *Andira* Lam., *Anthephora* Schreb., *Aptandra* Miers, *Asclepias* L., *Ascolepis* Nees, *Bartsia* L.*, *Bouchea* Cham.*, *Brachypterys* Juss. (?), *Brunnichia* Banks, *Buforrestia* C. B. Cl., *Cacoucia* Aubl., *Chlorophora* Gaud., *Chrysobalanus* L., *Conocarpus* Gaert., *Copaisera* L., *Corrigiola* L., *Drepanocarpus* G. F. Mey., *Echinodorus* L. C. Rich., *Genlisea* A. St Hil., *Guarea* Allem., *Heisteria* Jacq., *Heteranthera* R. et P., *Heteropteris* H., B. et K., *Hoffmannseggia* Cav., *Hydranthelium* H., B. and K., *Hymenocallis* Salisb., *Laguncularia* Gaert., *Lindackeria* C. Presl, *Macrolobium* Schreb., *Malouetia* A. DC., *Maprounea* Aubl., *Marica* Ker-Gawl., *Mayaca* Aubl., *Melasma* Berg.*, *Microtea* Sw., *Neurotheca* Salisb., *Olyra* L., *Parkinsonia* L., *Pentaclethra* Benth., *Prevostea* Choisy, *Priva* Adans., *Ptychopetalum* Benth., *Renealmia* L. f., *Rhipsalis* Gaert., *Saccoglossis* Endl., *Schaueria* Nees, *Schultesia* Mart., *Sclerocarpus* Jacq., *Sparganophorus* Crantz, *Sphaeralcea* A. St Hil., *Symmeria* Benth. et Hk., *Syngonanthus* Ruhl., *Talinum* Adans., *Tapura* Aubl., *Thalia* L., *Thamnosma* Torr. et Frem., *Trianosperma* Mart., *Trichopteryx* Nees, *Tristachya* Nees, *Trymatococcus* Poepp. et Engl., *Vismia* Vand., *Voyria* Aubl. and *Leiphaimos* Ch. et Sch.

3. America and Madagascar only.

Paepalanthus Mart., *Pedilanthus* Neck., *Ravenala* Adans., *Rheedia* L.

b. Africa, Asia and/or Madagascar etc.

1. Africa and Asia (often extending into Australasia and Polynesia).

Adenanthera L., *Adina* Salisb., *Aegle* Corr., *Alstonia* R. Br., *Ancistrocladus* Wall., *Anogeissus* Wall., *Antiaris* Lesch., *Aphania* Bl., *Argostemma* Wall., *Artanema* D. Don, *Baissea* A. DC., *Bourringia* Champ., *Brachylophon* Oliv., *Brucea* J. F. Mill., *Bryonopsis* Arn., *Cajanus* DC., *Calamus* L., *Centotheca* Desv., *Clausena* Burm. f., *Cleistachne* Benth., *Coccinia* W. et A., *Cyanotis* D. Don, *Cyrtococcum* Stapf, *Dalhousiea* R. Grah., *Dicanthium* Willemet, *Doryalis* E. Mey., *Drogmansia* De Wild., *Elatostema* Forst., *Elsholtzia* Willd., *Elytrophorus* Beauv., *Englerastrum* Briq.*, *Epithema* Bl., *Erythrophleum* Afzel., *Firmiana* Marsili, *Fingerhuthia* Nees, *Flacourtiea* Comm., *Flemingia* Roxb., *Flueggea* Willd., *Geissaspis* W. et A., *Halopegia* K. Sch., *Harrisonia* R. Br., *Hemigymnia* Stapf, *Heritiera* Ait., *Holarrhena* R. Br., *Hunteria* Roxb., *Hymenocardia* Wall., *Illigera* Bl., *Kaempferia* L., *Kedrostis* Medik., *Lasianthus* Jack,

Lecanthus Wedd., *Lepistemon* Bl., *Leptonychia* Turcz., *Limonia* L., and *Citropsis* Engl., *Mallotus* Lour., *Mansonia* J. R. Drum., *Microdesmis* Hk. f., *Mitragyna* Korth., *Monochoria* C. Presl, *Musa* L., *Naregamia* W. et A., *Neuropeltis* Wall., *Odina* Roxb., *Opilia* Roxb., *Oropetium* Trin., *Orthanthera* Wight, *Oxytenanthera* Munro, *Parochetus* Buch.-Ham., *Pergularia* L., *Perotis* Ait., *Petalidium* Nees, *Platystoma* Benth. et Hk. f., *Pterolobium* R. Br., *Pteygota* Schott et Endl., *Pygeum* Gaert., *Pyrenacantha* Wight, *Quisqualis* L., *Remusatia* Schott, *Rothia* Pers., *Sansevieria* Thb., *Sarcocephalus* Afzel., *Sauromatum* Schott, *Schoenfeldia* Kth., *Sesamum* L., *Shuteria* W. et A., *Stephania* Lour., *Strombosia* Bl., *Tenagocharis* Hochst., *Thelepogon* Roth, *Tiliacora* Colebr., *Tinospora* Miers, *Vossia* Wall. et Griff.

2. Africa, Madagascar etc. and Asia (often extending into Australasia and Polynesia).

Achyrospermum Bl., *Acridocarpus* Guill. et Perr., *Acrocephalus* Benth., *Adenia* Forsk., *Aerua* Juss.*, *Alangium* Lam. and *Marlea* Roxb., *Albizia* Duraz., *Alloteropsis* C. Presl, *Alysicarpus* Neck., *Amorphophallus* Bl., *Amphilophis* Trin., *Anisophyllea* R. Br., *Apodites* E. Mey., *Aponogeton* L. f., *Arduina* Mill. and *Carissa* L., *Artobotrys* R. Br., *Asteracantha* Nees*, *Asystasia* Bl., *Azima* Lam., *Baphia* Afzel., *Blepharis* Juss., *Blyxa* Nor., *Boottia* Wall., *Borassus* L., *Bridelia* Willd., *Bruguiera* Thou., *Canarium* L., *Canscora* Lam., *Centipeda* Lour., *Ceriops* Arn., *Ceropegia* L., *Cheirostylis* Bl., *Cirrhoptetalum* Lindl., *Cleistanthus* Hk. f., *Cnestis* Juss., *Coffea* L., *Commiphora* Jacq., *Corymbis* Thou., *Courtoisia* Nees, *Crossandra* Salisb., *Cryptolepis* R. Br. and *Ectadiopsis* Benth., *Deeringia* R. Br., *Dichrostachys* W. et A., *Dicoma* Cass., *Disperis* Sw., *Dumasia* DC., *Ebolium* Kurz, *Emilia* Cass., *Enalus* L. C. Rich., *Enteropogon* Nees, *Ethulia* L. f., *Exacum* L., *Filicium* Thwait., *Flagellaria* L., *Gaertnera* Lam., *Garcinia* L., *Gastonias* Comm., *Gelonium* Roxb., *Geniosporum* Wall., *Gerbera* L., *Gieseckia* L., *Gloriosa* L., *Gnidia* L. and *Lasiosiphon* Fres., *Grangea* Adans., *Grewia* L., *Gymnema* R. Br., *Gynura* Cass., *Haemarthria* Munro, *Helinus* E. Mey., *Holmskioldia* Retz., *Hydrilla* L. C. Rich., *Hydrophylax* L. f., *Hymenodictyon* Wall., *Hypoestes* Soland., *Iodes* Bl., *Iphigenia* Kunth, *Laggera* Sch.-Bip., *Laurembergia* Berg., *Lepironia* L. C. Rich., *Lumnitzera* Willd., *Macaranga* Thou., *Maesa* Forsk., *Medinilla* Gaud., *Memycylon* L., *Mezoneuron* Desf., *Micrangeria* Benth., *Micrococca* Benth., *Microglossa* DC., *Moschosma* Reichb., *Mundulea* Benth., *Mussaenda* L., *Myrsine* L., *Neyraudia* Hk. f., *Nothosaerua* Wight, *Oberonia* Lindl.,

Ochna Schreb., *Olax* L., *Olea* L., *Orthosiphon* Benth., *Osbeckia* L., *Paropsia* Nor., *Pavetta* L., *Pedalium* L., *Pemphis* Forst., *Peristrophe* Nees, *Phajus* Lour., *Phaylopsis* Willd., *Phoenix* L., *Pleurostylia* W. et A., *Pollia* Thb., *Polyalthia* Bl., *Premna* L., *Pseudarthria* W. et A., *Rhamphicarpa* Benth., *Rhinacanthus* Nees, *Rungia* Nees, *Saccolabium* Bl. and *Acampe* Lindl., *Satyrium* L., *Scolopia* Schreb., *Sebaea* Soland.*, *Secamone* R. Br. and *Toxocarpus* W. et A., *Smithia* Ait., *Sopubia* Buch.-Ham., *Sphaeranthus* L., *Stereospermum* Cham., *Striga* Lour., *Strophanthus* DC., *Tarenna* Gaert., *Thunbergia* Retz, *Toddalia* Juss., *Tricalysia* A. Rich., *Tristellateia* Thou., *Turraea* L., *Tylophora* R. Br., *Uraria* Desv., *Urophyllum* Wall., *Vangueria* Juss., *Vepris* Comm., *Voacanga* Thou. and *Orchipeda* Bl., *Wiesneria* M. Mich., *Woodfordia* Salisb., *Xylia* Benth.

3. Madagascar etc. and Asia (often extending into Australasia and Polynesia).

Actinoschoenus Benth., *Adenochlaena* Boivin, *Agrostophyllum* Bl., *Agyneia* L., *Apluda* L., *Atylosia* W. et A., *Barringtonia* Forst.*, *Bleekrodea* Bl., *Byrsophyllum* Hk. f., *Carallia* Roxb., *Cephalostachyum* Munro, *Cipadessa* Bl., *Cymbidium* Sw., *Ellertonia* Wight, *Erythrospermum* Lam., *Evodia* Forst. and *Melicope* Forst., *Geniostoma* Forst., *Givotia* Griff., *Melastoma* L., *Nepenthes* L., *Ochrocarpus* Thou., *Paederia* L., *Pongamia* Vent., *Pothos* L., *Samadera* Gaert., *Sandoricum* Cav., *Schizostachyum* Nees, *Strobilanthes* Bl., *Thuarea* Pers., *Vateria* L., *Wormia* Rottb., *Zoysia* Willd.

4. Africa and/or Madagascar etc. and Australasia.

Adansonia L., *Athrixia* Ker-Gawl., *Caesia* R. Br., *Cunonia* L., *Hibbertia* Andr., *Keraudrenia* J. Gay, *Rulingia* R. Br., *Triraphis* R. Br.

c. America and Asia (often extending into Australasia and Polynesia).

Anaxagorea A. St Hil., *Bocagea* A. St Hil., *Callicarpa* L., *Capsicum* L., *Clethra* Bert., *Engelhardtia* Leschen. and *Orecomunnea* Oerst., *Enhydra* Lour., *Gilibertia* R. et P., *Helicteres* L., *Ichnanthus* Beauv., *Inocarpus* Forst., *Klugia* Schlechd., *Laplacea* H. B. et K., *Lespedeza* L. C. Rich., *Linostoma* Wall. and *Lophostoma* Meissn., *Mappia* Jacq., *Meliosma* Bl., *Microtropis* E. Mey., *Mitreola* R. Br., *Oxybaphus* L'Herit., *Physurus* L. C. Rich., *Roucheria* Planch., *Sageretia* Brongn., *Sarcosiphon* Bl., *Saurauia* Willd., *Schoepfia* Schreb., *Sloanea* L. and *Echinocarpus* Bl., *Spathiphyllum* Schott, *Styrax* L., *Symplocos* Jacq., *Turpinia* Vent.

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d. America and Australasia only.

Distichis Thou., *Lindenia* Benth., *Nicotiana* L., *Orthosanthes* Steud., *Trichocline* Cass.*

e. Discontinuous over a considerable part of the tropical zone.

Arundinaria L., *Calliandra* Benth., *Campnosperma* Thwait., *Cochlospermum* Kunth, *Dioclea* H., B. et K., *Halophila* Thou., *Hermannia* L., *Jasminum* L., *Lochnera* Reichb., *Lonchocarpus* H., B. et K., *Mimulus* L., *Omphalea* L., *Passiflora* L., *Pilosyles* Guill., *Protium* Burm. f., *Schrebera* Roxb., *Stephanotis* Thou. and *Jasminanthes* Bl., *Stillingia* L., *Thalassia* Banks, *Turnera* L.

f. Anomalous genera of the tropical zone.

Canarina L., *Cossignia* Comm., *Cytinus* L., *Fagonia* L., *Kissenia* R. Br., *Nesogenes* A. DC., *Pelargonium* L'Herit., *Pharnaceum* L., *Phyllica* L., *Ruthea* Bolle.

C. GENERA FOUND ENTIRELY OR PREDOMINANTLY IN THE SOUTH TEMPERATE ZONE.

a. America and Australasia.

1. America, Australasia and New Zealand.

Abrotanella Cass., *Colobanthus* Bartl., *Discaria* Hk. f., *Donatia* Forst., *Drapetes* Banks, *Hebe* Comm., *Libertia* Dumort., *Lilaeopsis* Greene, *Nothofagus* Bl., *Oreomyrrhis* Endl., *Pernettya* Gaud. and *Gaultheria* L., *Schizilema* Domin, *Selliera* Cav., *Uncinia* Pers.

2. America and Australia or New Zealand.

Azorella Lam.*, *Embothrium* Forst., *Enargea* Banks, *Eucryphia* Cav., *Fuchsia* L., *Gaimardia* Gaud., *Griselinia* Forst., *Jovellana* R. et P., *Laurelia* Juss., *Marsippospermum* Desv., *Ourisia* Comm., *Phyllachne* Forst., *Rostkovia* Desv.

3. America and Australia and/or Polynesia.

Aristotelia L'Herit., *Cordyline* Comm., *Drimys* Forst., *Lomatia* R. Br., *Muchlenbeckia* Meissn.

b. Africa and Australasia only.

Arctotis L. and *Cymbonotus* Cass., *Australina* Gaud., *Bulbine* L., *Bulbinella* Kunth, *Byblis* Salisb. and *Roridula* L., *Chrysithrix* L., *Helipterum* DC., *Hypolaena* R. Br., *Moraea* Mill., *Restio* L., *Villarsia* G. F. Gmel., *Wurmbea* Thb.

c. Anomalous genera of the South Temperate Zone.

Carpobrotus N. E. Br., *Chevreulia* Cass., *Leptocarpus* R. Br., *Pringlea* Anders., *Tetragonia* L.

D. GENERA FOUND IN BOTH NORTH AND SOUTH
TEMPERATE ZONES

a. North Temperate Zone, and S. America, S. Africa and Australasia.

Erodium L'Herit., *Frankenia* L., *Geum* L., *Koeleria* Pers., *Myosotis* L., *Thesium* L., *Triglochin* L., *Viola* L., *Zostera* L.

b. North Temperate Zone, S. America and Australasia.

Calandrinia H., B. et K., *Caltha* L., *Coriaria* L., *Daucus* L., *Euphrasia* L., *Gentiana* L., *Glycyrrhiza* L., *Montia* L., *Myosurus* L., *Myrtus* L.

c. North Temperate Zone, S. Africa and Australasia.

Althenia Petit, *Emex* Neck., *Kochia* Roth, *Papaver* L., *Statice* Willd., *Trigonella* L., *Zygophyllum* L.

d. North Temperate Zone and S. Africa.

Cryophyllum N. E. Br., *Herniaria* L., *Oligomeris* Cambess., *Seetzenia* R. Br., *Sium* L.*

e. North Temperate Zone and Australasia.

Alisma L., *Angelica* L., *Damasonium* Mill., *Nitraria* L., *Posidonia* Ch. Koen., *Rochelia* R. et S. and *Maccoya* F. v. M., *Saussurea* DC., *Sparganium* L., *Veronica* L.*

f. North Temperate Zone and S. America.

Adenocaulon Hk. f., *Antennaria* Gaert., *Armeria* Willd., *Chrysosplenium* L., *Drusa* DC.*, *Empetrum* L., *Lardizabala* R. et P. and *Parvatia* Decne., *Lepuropetalon* Elliott, *Microcala* Hffmagg. et Link, *Phippia* R. Br., *Primula* L., *Saxifraga* L., *Sibthorpia* L.

E. GENERA OF VARIOUS DISTRIBUTION BUT ALL WITH OUTLYING
SPECIES IN THE HAWAIIAN ISLANDS.

a. Entirely or predominantly Old World.

Alphitonia Reissek., *Alyxia* Banks, *Antidesma* L., *Byronia* Endl., *Canthium* Lam., *Claoxylon* A. Juss., *Coprosma* Forst., *Cyatethodes* Labill., *Dianella* Lam., *Dracaena* L., *Embelia* Burm. f., *Exocarpus* Labill., *Freycinetia* Gaud., *Joinvillea* Gaud., *Korthalsella* van Tiegh., *Metrosideros* Banks, *Myoporum* Banks et Soland., *Ochrosia* Juss., *Osteomeles* Lindl., *Pandanus* L., *Pelea* A. Gr., *Pipturus* Wedd., *Pittosporum* Banks, *Plectranthus* L'Herit. and *Coleus* Lour., *Strongylodon* Vog., *Suttonia* Hk. f., *Tetraplasandra* A. Gr.

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b. Entirely or predominantly New World.

Cuphea Adans., *Hesperocnide* Torr., *Nama* L., *Sicyos* L., *Syrrinchium* L., *Sphacele* Benth.

c. Both Old and New Worlds.

Acaena L., *Astelia* Banks et Soland., *Eurya* Thb., *Gunnera* L.,
Lagenophora Cass., *Lysimachia* L., *Nertera* Banks et Soland., *Oreobolus* R. Br., *Osmanthus* Lour., *Perrottetia* H. B. et K., *Pritchardia* Seem. et H. Wend., *Urera* Gaud.

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SOME VASCULAR ABNORMALITIES IN THE AERIAL STEM OF *PSILOTUM TRIQUETRUM*

By H. S. HOLDEN

THE stelar anatomy of the normal aerial stem of *Psilotum triquetrum* has been worked out by a number of investigators (1, 3, 8) and is now so well known that it requires only a brief description in connection with the present observations.

The stele, at its base, possesses a more or less cylindrical core of tracheids with a slight admixture of parenchyma, the whole being surrounded by phloem. At a slightly higher level the intraxyllic parenchyma is concentrated to form a fairly compact pith whilst the protoxylem, which at lower levels is ill-defined, becomes readily distinguishable. This stage is succeeded by one in which the pith becomes wholly sclerised and in which the xylem possesses a stellate outline as seen in transverse section, the projecting points being occupied by the protoxylem. At this level the number of protoxylem groups in stout stems varies from eight to ten, this condition being derived, according to Boodle (3), from an originally diarch condition at the base of the stem.

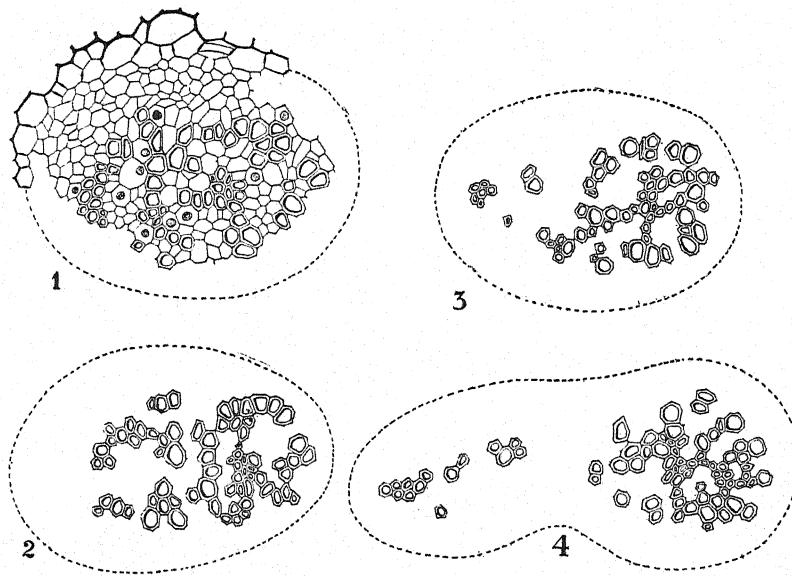
Tracheids of secondary origin may occur locally, notably at and near the lower parts of the aerial stem (2, 3, 8).

The branching is essentially dichotomous though occasional trichotomy is recorded both by Solms-Laubach (12) and by Miss Ford (8). No anatomical details of these exceptional cases are given by either author and it is possible that they are to be interpreted as the result of an extremely precocious division of one of the shanks of a dichotomy. Where dichotomy occurs subsequent to the assumption of a definitely exarch position of the protoxylem, the stele undergoes a widening in the plane of the dichotomy followed by median constriction and the separation of two independent daughter steles. The division is accompanied by the development of new protoxylem groups in the contiguous portions of the two daughter steles (1, 3, 8).

The stelar tissues are surrounded by a well-marked primary endodermis which shows up very clearly in unstained sections mounted in Canada balsam. The endodermis is figured more or less conventionally by Bertrand (1), the Caspian strip being indicated by dots on the radial walls, but Miss Ford's figures (8) Pl. XXXIX,

figs. 8 and 10), in which it is shown completely covering the radial wall, are more in accord with my observations. The radial width of the Caspary strip is, however, subject to some variation and a small portion of the radial walls of the endodermal cells may remain unmodified.

The vascular abnormalities which form the subject of these notes occurred in two stems which will be described separately. In the first there was no external evidence of modification apart



Figs. 1-4. Series of transverse sections of the stele of the first stem from below upwards showing the bifurcation of the xylem. A portion of the phloem and endodermis is shown in Fig. 1, xylem and endodermis only shown in Figs. 2-4, the position of the endodermis being indicated by a dotted line. ($\times 200$.)

from a slight flattening of the stem near its base. A series of sections was cut passing completely through the flattened portion and yielded rather surprising results. Near the base of the series the central mass of tracheids and parenchyma became ovoid as seen in transverse section (Fig. 1), and this was followed by a stage in which indications of a median constriction of the xylem were present (Fig. 2). Although one xylem mass was somewhat less than its fellow the general appearance suggested an early stage in a dichotomy but at a higher level the tracheids constituting the smaller xylem mass

became reduced in number (Fig. 3) and at the same time gradually moved away from the larger mass (Fig. 4). Subsequent to the separation the smaller tracheidal group rapidly dwindled and ultimately disappeared. The endodermis, though showing a median constriction at the region of widest separation of the two xylem masses, soon loses this feature, following the disappearance of the group. For a time it encloses an ovoid stele in which the single compact xylem strand is eccentrically situated but it rapidly moves inward, thus producing a cylindrical stele roughly similar to that at the base of the series. It is rather interesting to note that, whilst

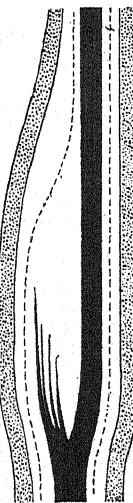


Fig. 5

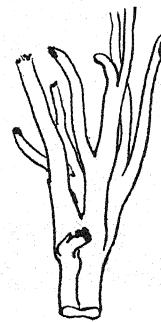


Fig. 6

Fig. 5. Diagrammatic vertical section of the first stem. Xylem in solid black, endodermis shown by dotted line, brown-walled cortical tissue stippled.

Fig. 6. Drawing of the second stem to show the crowded dichotomies. ($\times 1$.)

the cells of the inner cortex, with their curiously modified, thick, brown walls, keep pace with the expansion of the stele, they move inward again more slowly than the endodermis, so that a strip of cortical tissue with colourless walls lies to one side of the stele between the endodermis and the zone of modified cells. An attempt to indicate the salient features of this stem as they would appear in longitudinal section is shown in Fig. 5.

The second stem, showing vascular abnormality, was a short piece resembling a miniature "Witches' Broom," this appearance being due to a series of successive and somewhat unequal dichotomies (Fig. 6). Nearly all the branchlets showed evidence of apical injury

and discolouration which appeared to be due to some mechanical cause.

Serial sections of this stem were made from below upwards and a selection of these is shown diagrammatically in Fig. 7 *a-f*. At its base the piece of stem, which had a major diameter of 4.5 millimetres, showed three steles, two of which were obviously the result of a recent dichotomy whilst the third was widening preparatory to bifurcation. The constituent steles showed a number of features of interest, the two most noteworthy being (i) the local occurrence of secondary tracheids accompanied by a suggestion of radial arrangement in the adjacent parenchyma, and (ii) the curiously defective character of the core of sclerenchyma which is normally present. In each of the steles the sclerenchyma is replaced to a greater or less extent by thin-walled elements, though the reason for this is somewhat obscure. It is possible, however, that the rapid production of the numerous branchlets has induced a lag in the rate of differentiation of the intraxylic sclerenchyma.

In addition to the features to which reference has been made above a further peculiarity was the occurrence on the inner side of one of the paired steles of a small accessory stele consisting of a group of three tracheids surrounded by phloem and endodermis (Fig. 7 *a, st.*). This, on being traced upwards, lost, first its xylem and then its phloem, ultimately ending blindly in the parent cortex. Happily four further examples of a similar kind were furnished by the complete series of sections so that their entire history could be traced. In every case they are initiated by the radial elongation of one of the wedge-shaped xylem masses, the tip of which becomes detached and is ultimately nipped off as a separate strand with its own endodermis. Having attained independent status it gradually dwindles out, frequently undergoing lateral displacement before it disappears. Fig. 8 illustrates at *A* and *B* two stages in the giving off of these accessory strands from the main strand *A* shown in Fig. 7 *a-c* and also indicates the imperfect development of the intraxylic sclerenchyma.

The chief changes undergone by the main stelar groups are illustrated in Fig. 7 *a-f*. The two lower steles, which may be designated *A* and *A'*, have the form of four-pointed stars in the lowest sections cut and they retain this character until each undergoes dichotomy. The result of the dichotomy is the formation of two independent diarch steles each of which is destined to be the vascular supply of one of the slender branchlets. The division of the parent

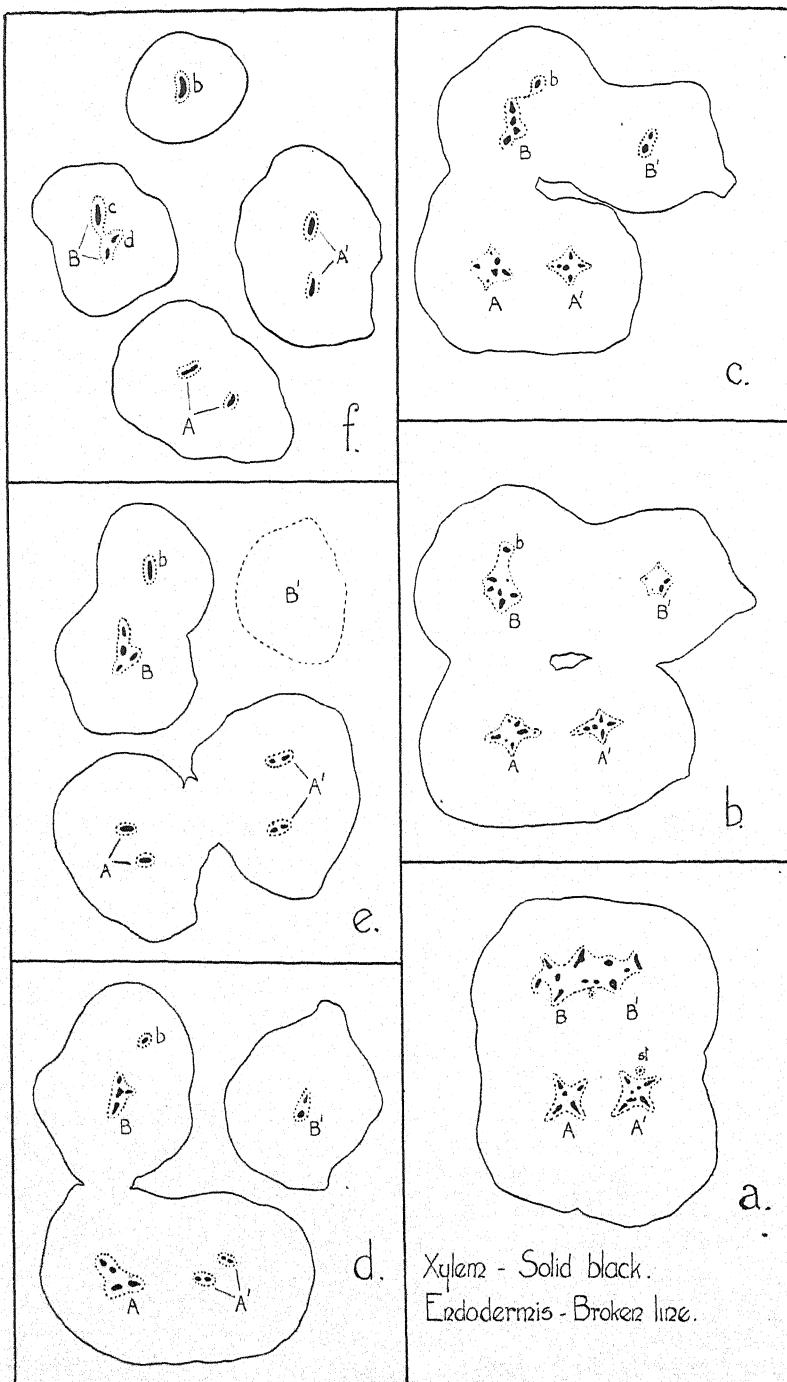


Fig. 7 *a-f.* Series of camera-lucida outlines of transverse sections of the second stem from below upwards showing the distribution of the vascular strands to the branches. The position of the withered tip of one branch is shown by an area enclosed by a broken line at *B'* in Fig. 7 *e.* ($\times 6.$)

stele appears to involve a change in the orientation of the constituent xylem groups (cf. Fig. 7 c, d, e) and does not involve the initiation of new xylem poles such as occurs in the course of dichotomies at lower levels.

The upper stele, which is obviously about to undergo dichotomy, gives off a small, blindly-ending strand of the type described above prior to bifurcation. The two daughter steles, *B* and *B'*, are five-rayed (Fig. 7 b), one of these being more robust than the other. This stele (*B*) almost immediately gives off a bipolar strand (*b*) which gradually becomes independent and later constitutes the

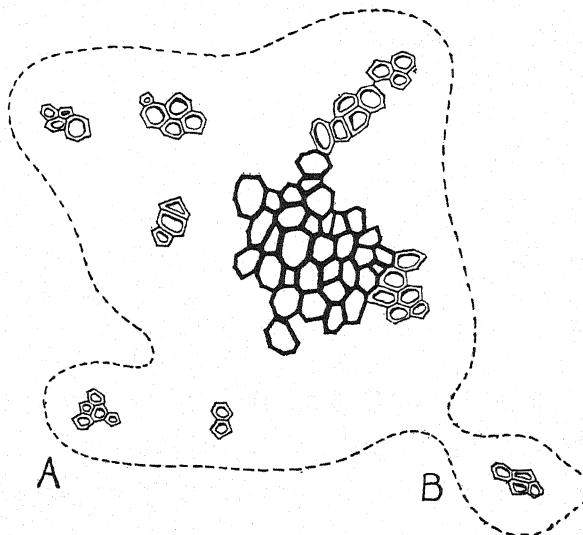


Fig. 8. Stele *A* showing the disposition of the xylem and intraxyllic sclerenchyma. Leaf-traces are being given off at *A* and *B*. This figure is from a section intermediate in position between Figs. 7 b and 7 c. ($\times 300$.)

vascular supply of one of the branchlets (7 f). At a higher level the remainder of the stele undergoes a further division into two (7 d-f), these again being destined to supply separate branchlets. The two strands are shown at a stage in which they are just linked together by a narrow endodermal neck in Fig. 7 f.

The fate of the weaker stele (*B'*) is quite different since three of its five rays become reduced (Fig. 7 b) and die out, the two persistent rays constituting the vascular supply of a single stout branchlet (Fig. 7 c, d). It is worthy of note that, with one exception, the vascular supply to each of the branchlets is initiated as two separate

xylem groups enclosed in a common phloem and that their union to form a continuous band may be delayed for quite a considerable vertical interval.

The most exhaustive study of the mode of branching of *Psilotum triquetrum* is that made by Bertrand (1) who has evolved a somewhat complex system of classification to which he considers the various types of axis, both subterranean and aerial, conform. Subsequent workers do not consider, however, that the various categories of axis can be differentiated with a precision sufficient to justify the somewhat inflexible system which Bertrand has put forward. It is interesting to observe that this author records the occasional formation of unequal branches as a result of dichotomy (1) p. 162) and notes that the weaker branch, with its smaller and simpler vascular system, may sometimes atrophy and undergo lateral displacement.

In addition to this condition Bertrand also describes one which he interprets as a sympodial cladode system, this being characterised by the fact that, at intervals, small bipolar traces are given off from the main stele which pass rapidly to the exterior where they are associated with aborted apices (1) pp. 165-166). There does not seem to be any adequate reason why the condition just described should not be regarded as a series of unequal dichotomies in which the weaker branch is constantly displaced and undergoes abortion. Such an interpretation would seem to follow logically from the type of structure described in the previous paragraph.

It should be noted, however, that Solms (12) records the occurrence of normal lateral branching in addition to dichotomy.

The first of the specimens described in the present paper seems to be most readily interpreted as a dichotomy the weaker shank of which has aborted at a very early stage. This interpretation receives support from the behaviour of the stele itself since this shows division into two practically independent portions. It is moreover a stage which might be reasonably anticipated in a reduction sequence, the earlier stages of which have already been indicated by Bertrand (1). Such a sequence would read as follows: (i) Equal dichotomy, (ii) Unequal dichotomy, (iii) Unequal dichotomy with lateral displacement of the weaker branch, (iv) Unequal dichotomy with lateral displacement and subsequent abortion of the weaker branch, (v) Incomplete dichotomy with rapid abortion of the weaker branch.

With regard to the second specimen there seems no doubt that the main factor in the stelar disturbance is that of the rapidly superposed dichotomies. The chief features resulting from this are fairly

easy to recognise and interpret. The emission of the small, blindly-ending traces from the tips of the xylem rays is however rather a surprising peculiarity. Although the minute leaves of *Psilotum triquetrum* are normally without a vascular supply it seems probable that these small strands are leaf traces which, to use the terminology of the Harvard school, have been "recalled" by the stimulus which has induced the rapid branching. In this connection it should be noted that, whilst both Bertrand(1) and Miss Ford(8) describe the leaf as being without vascular supply, Pritzel(10) records the occasional occurrence of vestigial traces in this species. In the allied *P. flaccidum* the leaf-trace is well developed and in the description of this species by Stiles(13) the mode of origin and general behaviour of this strand are so like those of the small strands here described for *P. triquetrum* as to leave no doubt as to their homology. It is noteworthy that even in *P. flaccidum* the vascular tissue is not continued into the leaf but stops short at the level of leaf-insertion. The leaf-traces in this species also appear to differ from the similar strands now recorded as occurring in *P. triquetrum* in the fact that the endodermis is not invariably well-defined though this is a point upon which further observations are desirable. The fact that a leaf-trace is normally present both in the nearly related genus *Tmesipteris* and in a closely allied species of *Psilotum* itself indicates that its absence in *Psilotum triquetrum* is a secondary condition and one due to reduction since it is difficult to believe that any stimulus, traumatic or otherwise, would so hasten the evolutionary development of the species as to induce the production of a new feature of so important a character.

SUMMARY.

1. The anatomy of portions of two aerial stems of *Psilotum triquetrum* showing vascular abnormality is described.
2. In the first of these the stele becomes ovoid and then undergoes incomplete bifurcation, one of the daughter steles so produced dwindling and ultimately aborting while the other persists. It is suggested that this condition represents a case of almost complete suppression of one shank of a dichotomy.
3. In the second case the stem, which at its upper end divides into a large number of small irregularly grouped branches, contains three independent main steles, the largest of which subsequently undergoes bifurcation. The vascular supply of the branches is derived from these main steles by subdivision.

4. The main steles show a small amount of secondary xylem locally and the core of intraxylic sclerenchyma is, in part, replaced by parenchyma.

5. They give off a number of small traces from the tips of the xylem arms which, from their close resemblance to the leaf-traces of the allied species *Psilotum flaccidum*, are held to be leaf-traces also, although such strands are not normally present in *P. triquetrum*.

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LABORATORY NOTES

USEFUL DEVICES FOR THE TEACHING OF
ELEMENTARY PLANT PHYSIOLOGY

By B. BARNES

I. *To investigate the changes produced in the air by a flame and by green plants.*

IT has been found that the apparatus recommended by MacDougal (1916) for investigating the changes produced in air by a flame, and by green plants, seldom gives a satisfactory result. The failures are due to water transpired by the plant; condensed water spoils the match and the striking surface, and the wick of the candle, left in a porous condition by the expiring flame, becomes so wet that, even if the match strikes, the wick will not ignite.

Improvements have been effected by using a "strike anywhere" match coated with a thin layer of paraffin wax, a piece of roughened tin for the striking surface, and a second candle, with a thick coating of wax on its wick. These modifications reduce the number of failures, but the manipulation is awkward, and the match often breaks. This difficulty has been overcome by the adoption of an electrical method of ignition (Fig. 1).

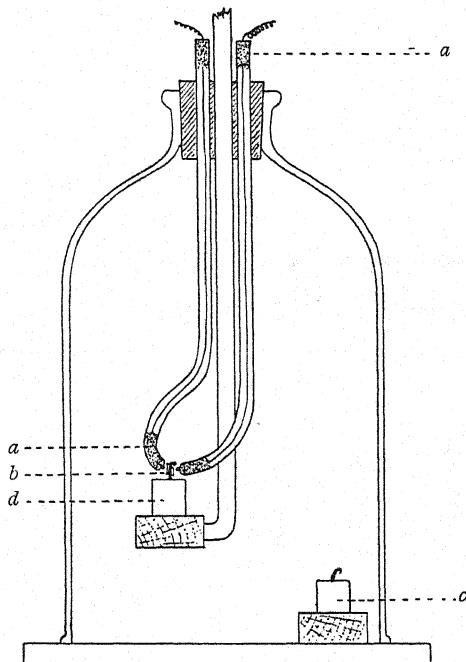


Fig. 1. Bell jar arranged for the electrical ignition of the candle; the plant is omitted for the sake of clearness. *a*, seals of paraffin wax; *b*, chip of celluloid; *c*, first candle; *d*, second candle.

A soft, well-waxed natural cork is fitted to the tubulure of a large bell jar. Through two holes in the cork, narrow glass tubes are passed, carrying each a copper wire, sealed in with paraffin wax; the tubes are bent in such a way that their lower ends can be brought to form a spark gap of about one centimetre in length. Through a third hole in the centre of the cork, a piece of stout glass rod is passed; its upper end stands some five or six inches above the cork, and its lower end is bent in such a way that the rod will carry a small flat cork in a horizontal position. The cork bears a short candle, whose wick is coated with wax, containing a chip of celluloid.

It is necessary to insert the tubes and rod from below, after the cork has been placed in the tubulure; the parts are adjusted so that the wick of the candle lies in the spark gap, or can be readily brought into it, by lateral pressure on the upper, projecting part of the rod.

A potted plant and a lighted candle are arranged on a thick glass plate. The prepared bell jar is carefully lowered around them, and sealed to the plate; this may be done by means of a mixture of equal parts of bees' wax, tallow and vaseline, applied warm. The flame soon expires, and the apparatus is set aside for some hours, in good light.

When it is desired to light the candle, the upper ends of the two copper wires are connected with a large induction coil, and as many accumulators as are required to give a strong spark. Any adjustments necessary to bring the wick into the spark gap are made, and the circuit is closed; it is well to press the bell jar down to the plate, to prevent unsealing when the celluloid ignites.

This method gives good results. It is true that the use of two candles is a slight objection, but no other convenient and reasonably simple way has been found of overcoming the trouble caused by the wetting of the porous wick left when the flame slowly expires. Efforts to dry the wick by exposure to the spark have not been found satisfactory.

II. *To investigate the decrease in weight of a transpiring plant.*

Difficulty is often encountered in making a satisfactory joint when sheet rubber or tin foil is wrapped around a pot in which a plant is growing, in order to prevent loss of water by evaporation. This difficulty may be met by re-potting the plant in a non-porous receptacle (jam pots do well), and then after drying the stem of the plant and the lip of the pot, sealing with a layer of paraffin wax, about one centimetre in thickness. A wax of M.P. 47° F. has

been found to work well, and to cause no apparent injury to plants of *Vicia Faba*, provided that it is warmed in a water-bath to a temperature only just sufficient to melt it.

III. *The relation between the supply of carbon dioxide and the evolution of oxygen.*

A quantity of *Elodea* is placed in a flask, to which is fitted a rubber cork carrying a small funnel, with the stem cut off square and inserted so that it does not project below the lower surface of the cork (Fig. 2). The flask is filled completely with water, and sufficient water is placed in the funnel to seal the mouth of an inverted test tube filled with water from the same sample as that used in the rest of the apparatus; the water may be charged with carbon dioxide, or deprived of that gas, by the usual means. A thin layer of oil floated over the free surface of the water in the funnel, will check gaseous interchange with the atmosphere. This form of apparatus has been found more serviceable than the simpler form, in which a test tube is inverted over the stem of a submerged funnel, and it is superior to those forms in which there is a delivery tube for the evolved gas, as there are no traps to retain the oxygen.

These devices have been used for several years in the teaching of elementary plant physiology, in the Department of Botany, Birkbeck College, University of London.

February, 1927.

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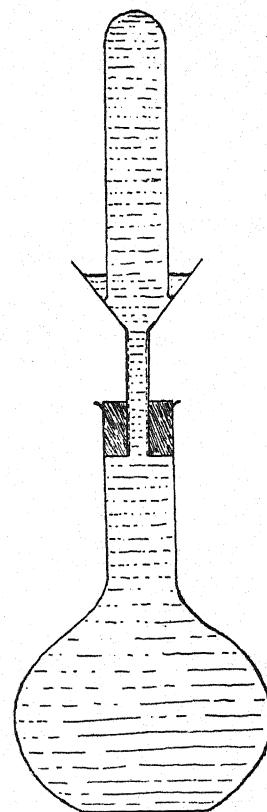


Fig. 2. Apparatus for investigating the relation between the supply of carbon dioxide and the evolution of oxygen.

FIFTH INTERNATIONAL BOTANICAL CONGRESS, CAMBRIDGE, 1930.

(Communicated.)

At the International Congress of Plant Sciences (Fourth International Botanical Congress) held at Ithaca, N.Y., United States of America, in August, 1926, an invitation was conveyed from British Botanists for the Fifth International Botanical Congress to be held in England in 1930. The invitation was accepted by the Botanists assembled at Ithaca, and arrangements are now being made for the Congress to be held at Cambridge about the middle of August, 1930.

An Executive Committee has been formed to make arrangements for the Congress, consisting of Dr F. F. Blackman, Prof. V. H. Blackman, Dr E. J. Butler, Prof. Sir John Farmer, Prof. F. E. Fritsch, Prof. Dame Helen Gwynne-Vaughan, Dr A. W. Hill, Prof. W. Neilson Jones, Sir David Prain, Dr A. B. Rendle (Treasurer), Prof. A. C. Seward (Chairman), Prof. W. Stiles, and Prof. A. G. Tansley.

It has been decided to organise the Congress in the following seven sections: Morphology (including Anatomy), Palaeobotany, Plant Geography and Ecology, Taxonomy and Nomenclature, Genetics and Cytology, Physiology, and Mycology and Plant Pathology.

Mr F. T. Brooks, the Botany School, University of Cambridge, England, and Dr T. F. Chipp, Royal Botanic Gardens, Kew, England, have been appointed Honorary Secretaries of the Congress, and any communications with regard to the Congress should be addressed to one or other of the Secretaries.

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STUDIES IN THE ECOLOGICAL EVOLUTION
OF THE ANGIOSPERMS

By J. W. BEWS, M.A., D.Sc.

CHAPTER VI

THE EFFECT OF CLIMATIC DIFFERENTIATION
ON DERIVATIVE TYPES

WE have seen how, under the influence of the biota, during long-continued favourable conditions, various derivative types of plant form have been produced. The effect of drier and colder conditions have been referred to continuously throughout, but it is now necessary to consider in greater detail the effects of the process of climatic differentiation on the non-woody forms. Schimper's classification of vegetation into three types, woodland, grassland and desert, is fundamental. Of these, woodland, according to our view, is relatively primitive, grassland and desert both derivative. The analysis of vegetation has, of course, proceeded very far since Schimper's time. Schimper regarded woodland and grassland as antagonistic types. "Woodland and grassland stand opposed to one another like two equally powerful but hostile nations, which in the course of time have repeatedly fought against one another for the dominion over the soil." A clearer understanding of plant successions, however, has shown that, while grassland in forest climatic areas may form a stage in the plant succession and ultimately be ousted by forest, yet in other areas it represents a climax stage. A grassland stage in the plant succession to forest may be a necessary stage as much as the youth of an individual is necessary before adult development can be reached. To speak of warfare between stages of the plant succession is unnecessary and misleading. In various plant successions stages succeed one another usually more or less as follows: (a) Open colonising stages consisting of ruderal, often annual, species, and xerophytic forms; (b) Xerophytic deep-rooted grasses; (c) Mesophytic grasses; (d) shrubs; (e) Low-growing,

much-branched, light-demanding trees; (f) Tall trees able to endure shade in their juvenile stages.

Now in the relatively favourable climatic areas the full succession may be shown. In less favourable areas the succession may stop at any of the stages, down to the first opening stage in desert regions. As already mentioned, the separate stages are roughly the reverse of the order of evolutionary development of plant forms. We have already dealt with the climax and subclimax stages dominated by woody plants which are the most primitive.

We must now deal with the earlier stages, and since grassland types play such an important part it is necessary to consider in some detail the evolutionary history of the grasses themselves.

THE FLORISTIC DIFFERENTIATION OF THE GRASSES

That the Gramineae are allied to the Cyperaceae appears to be without doubt, though it is possible that the two families may have been developed from ancestral forms (possibly forms like the Juncaceae) along parallel lines. The sedges, on the whole, have not progressed so far as the grasses, and are still more or less confined to primitive types of habitat. The views of various writers on the history of the Glumiflorae as a group do not help us much. Wettstein (1898) derives them from the Helobiae, through the Liliiflorae, with other groups such as the Scitamineae representing parallel or diverging lines of development. Schumann (1904) points out their similarity in vegetative characters to the Zingiberaceae among the Scitamineae. Lotsy (1911) derives the two families separately from a group like the Juncaceae among the Liliiflorae. Metz and his co-workers (1924), on serological grounds, look on the Glumiflorae as derived from the advanced Liliiflorae close to the point of origin of the Scitamineae. Sargent and Arber (1915) have carried out extensive work on their seedling anatomy which tends to confirm their origin from the Liliiflorae. We need not pursue this uncertain subject further. All the views that have been held would favour an origin for the grasses in hygrophilous warm habitats.

Hackel's work in Engler and Prantl's *Pflanzenfamilien* still remains the basis of all modern systems of classifying the grasses. The Gramineae, however, from the systematic standpoint are a difficult group. The limits of the tribes are none too well defined, and their inter-relationships are rather uncertain. The order of arrangement of the tribes adopted by Hackel is certainly not a phylogenetic one. It may be doubted whether the separation of the

tribes into two series—the first with the spikelets reduced and falling from the rachis entire, and the second with the spikelets often many flowered and with the rachilla articulated above the empty glumes—is by any means a natural subdivision.

In any case it is the second series which contains the most primitive forms, since reduction in the number of flowers in the spikelet has almost certainly been one of the main evolutionary trends. While the reduction is universal among the tribes included in Hackel's Series I it occurs also fairly commonly in Series II. It is a process which has taken place like so many general evolutionary trends, within many narrow circles of affinity. Hackel places the bamboos at the end of his second series, yet clearly the bamboos are floristically primitive.

Though it is easy to criticise Hackel's arrangement, and it has been modified in detail by Stapf and others, yet when any attempt is made to initiate any drastic changes in the grouping of the genera the difficulties are very great.

The tribes themselves are probably as natural as they can conveniently be made. We shall content ourselves, therefore, with an examination of some of the evolutionary trends within them and a few remarks on their probable ecological interrelationships and differentiation.

The Bambuseae are a very distinct tribe with woody, rarely herbaceous culms, and with the leaf-blade often with a short slender petiole, articulated with the sheath, from which it finally separates. Their flowers come nearest to the ordinary monocotyledonous type. There are usually three large perianth segments (or lodicules) which are very seldom wanting. The stamens are often six in number, sometimes more. In some genera the filaments are united in a tube. There are often three styles. The fruit in the Dendrocalameae and Melocanneae is a nut or berry instead of a caryopsis.

The bamboos are distributed somewhat unevenly throughout the tropical zone. Generally they are found outside of or surrounding the rain-forest areas. The monsoon region of Asia is particularly rich in species, but they are common in tropical America and less common in Africa. They have penetrated into subtropical regions and even into temperate regions. All through the tropics they tend to produce mountain types. In the Himalayas they ascend to an altitude of over 10,000 feet and still higher in the Andes. In Ecuador *Chusquea aristata* reaches the snow line. In their ecological differentiation some are tree forms, and they may occur, not in

clumps, but isolated, e.g. *Melocanna bambusoides*, a tall tree which has a fleshy apple-like fruit 8-12 cm. in diameter and seeds the size of betel nuts. The majority have short underground rhizomes which send up numerous culms forming clumps. Some species are climbers, e.g. species of *Arthrostylidium*, *Arthrostachys*, *Merostachys*, *Chusquea*, *Bambusa*. Finally there are a number of herbaceous forms, e.g. *Puelia* and *Atractocarpa* in Africa and *Planotia* in South America (on the elevated plains of Colombia). *Planotia* is described by Hackel as having long narrow panicles, with small numerous spikelets, of the same structure as those of the nearly allied *Chusquea*, and the habit of the Festuceae, with herbaceous, almost leafless culms and leaves crowded together close to the ground. The leaves are usually continuous, not articulate, with the sheath. *P. nobilis* has the largest leaves of any grass (1.5-4.5 m. long by 8.30 cm. broad). It is important to note further that several of the climbers (*Arthrostachys*, *Microstachys* and *Chusquea*) as well as the herbaceous *Planotia* show floristic advance in having the stamens reduced to three, the fruit a true caryopsis and the spikelets one-flowered.

Though the Bambuseae, therefore, are in many ways somewhat isolated, yet the gap between them and the Festuceae is not so very great. Herbaceous members like *Planotia* help to bridge it over, and it is very interesting again to find that the transition from the tropical types to temperate takes place on mountain ranges.

Apart from its possible connections with the primitive Bambuseae, the tribe Festuceae in its widest sense as defined by Hackel has chief claims to be considered the most primitive of the ordinary grasses, though even within this tribe certain conspicuous evolutionary advances have been made. In the subtribe Arundineae the genera *Phragmites* and *Arundo*, or forms very like them, go back to the Cretaceous. *Arundo* has many-flowered spikelets, almost woody stems, and broad flat leaves. These tall-growing hygrophilous types are generally distributed through the warmer regions of the world, recalling the bamboos in many of their features, but the common reed grass (*Phragmites communis*) is cosmopolitan. Reactions to drier conditions within the tribe are seen in the genera *Ampelodesmos* of the Mediterranean region and in *Gynerium*, the Pampas grass of South America. The subtribe Centotheceae have their leaves broad and net-veined, and include half a dozen small genera from various parts of tropical Africa, Asia and America (in the case of *Lophatherium* reaching Japan). In the Eu-Festuceae the large genera *Poa* and *Festuca* are well represented on the mountain regions of

the tropics, and have played an important part in establishing the dominance of the meadow grass or sod-forming type in cold temperate regions. The same subtribe shows advances in other genera, especially in the adoption of the annual habit, e.g. in such genera as *Schismus*, *Sclerochloa*, *Wagenheimia* and *Lamarckia* as well as in species of *Briza*, *Brizopyrum*, *Poa*, etc., in various xerophytic types, e.g. *Lasiochloa*, or halophytic types, e.g. *Aeluropus* and *Atropis*.

The other subtribes must be passed over with the briefest possible reference. The Pappophoreae are mostly tropical, but include many forms which have reached to dry conditions, e.g. *Pappophorum*, *Schmidtia*, *Triraphis*. The Sesleriae similarly include creeping grasses of the seacoast (*Monanthochloë*), low grasses of elevated plains (*Munroa*), annual steppe or desert grasses (*Am-mochloa*, *Urochlaena*), xerophytic forms (*Fingerhuthia*) and alpine grasses (*Sesleria*, *Oreochloa*). The Eragrosteae and Triodiaceae include several genera important in drier subtropical and temperate grasslands, *Triodia*, *Diplachne*, *Molinia*, *Eragrostis*, *Koeleria*. The Meliceae have a few small genera: *Ectrosia* and *Heterachne* in Australia, *Harpachne* in tropical Africa, *Anthochloa* in the Andes, *Diarrhena* in Japan and North America, and the large genus *Melica* throughout the temperate zones and mountains of the tropics except Australia.

The Brachypodieae (*Bromus*, *Brachypodium*) are also temperate or mountainous in distribution.

In brief, the Festuceae in general show primitive connections with hygrophilous tropical vegetation in the Arundineae and other forms, but as a whole have become highly differentiated first of all probably on mountain ranges of the tropics and subtropics but later to suit most of the highly diverse modern climatic habitats, both in drier subtropical areas and in temperate regions.

The tribe Aveneae, like the Festuceae, have some claims to being considered primitive, indeed the two tribes Aveneae and Festuceae might be grouped together. From their study of the anatomy of embryos and seedlings Sargent and Arber (1915) place *Avena* as nearest to their hypothetical ancestral form, but the number of forms dealt with were not very many and further work is needed. Within the tribe there is a general tendency to reduce the number of flowers in the spikelet to two, and one genus, *Holcus*, of temperate and mountainous distribution, has the spikelets readily deciduous as a whole, as in the tribes belonging to the first series of Hackel. Several of the genera of the Aveneae are temperate or mountainous, South African or Australian, e.g. *Danthonia*, *Pentaschistis*, *Achneria*.

These genera in South Africa mix with the sclerophyllous shrubs, and are abundant without ever assuming dominance. The warm temperate flora of Africa and Australia, we have already noted, has many ancient characteristics. As we have seen, the flora of the Mediterranean shows many connections and here again the Aveneae are represented by special genera, e.g. *Antinoria*, *Molineria*, *Aiopsis*, while the larger genera are more widespread, e.g. *Aira*, *Deschampsia*, *Trisetum*, *Avenastrum*, *Arrhenatherum* extending into the cold temperate regions and, like the heathers, some of them being especially characteristic of moorland areas. Not only in the dominant evergreen shrubs, therefore, but also in the associated grasses the connections between the ancient mountain flora of Africa, the flora of the Mediterranean region and the moorland flora of cold temperate Europe are well marked. The Aveneae also include a few tropical or subtropical genera, e.g. *Coelachne*, *Tristachya*, *Trichopteryx*, adapted to dry grassland conditions, and numerous annual species of *Avena* in the temperate regions.

Other tribes of the second series are all probably more advanced than the Festuceae and Aveneae. The Hordeae have the spikelets arranged in an equilateral spike, and the genera are all somewhat specialised, including many annual or ruderal perennial forms, e.g. species of *Lolium*, *Triticum*, *Hordeum*, *Agropyrum*, sand-dune species, e.g. *Elymus arenarius*. The subtribe Nardeae includes only one species, *Nardus stricta*, which has the spikelets one-flowered, the spikes unilateral, and only one stigma, being in many ways the most advanced type of all. Its distribution in Europe and northern Asia is, therefore, again very interesting from our present standpoint.

The Chlorideae have one-sided spikes or racemes and include important prairie grasses of North America (e.g. *Bouteloua*, *Buchloë*), seashore types (e.g. *Dactyloctenium*, *Spartina*), important creeping surface-rooting types (e.g. *Cynodon*), ruderal grasses (e.g. *Chloris*, *Eleusine*), xerophytic or mountain forms (*Microchloa*, *Harpechloa*, *Tripogon*, *Tetrachne*).

The Agrostideae have the spikelets regularly one-flowered and include the subtribes Stipeae, Phleoideae and Euagrostae. Of these the Euagrostae are the least specialised, and include the large genus *Agrostis* with over a hundred species distributed over the entire globe, but most frequent as meadow grasses in the northern hemisphere. *Ammophila arundinacea*, a sand-dune species, also belongs here.

The genus *Sporobolus* with over 80 species includes prairie grasses, ruderal grasses, xerophytic subtropical grasses and one widespread halophyte, *S. pungens*. The Phleoideae have a number of Mediterranean genera (*Cornucopiae*, *Crypsis*, *Heleochoea*, *Maillea*), a dwarf Arctic polar grass (*Phippia*), and the larger temperate genera *Alopecurus* and *Phleum*. The Stipeae include some forest grasses (e.g. *Milium effusum*, *Stipa dregeana*) but in general the great genus *Stipa* with over 100 species is adapted to grassland conditions. *Stipa pennata*, *S. tirsia* and *S. capillata* are the most important grasses of the Russian steppes. The genus *Stipa* is also prominent in the North American prairies. *S. tenacissima* is the esparto grass of Spain and North Africa. The genus *Aristida* is equally important, containing about the same number of species. *Aristida* is the most important genus of xerophytic grasses in the early stages of the plant succession in most regions of subtropical grasslands and (in the section *Stipagrostis*) in all the semi-desert and desert regions of Africa and western Asia. In view of what has already been said regarding the general course of evolutionary differentiation and its relationship to the plant succession it is particularly interesting to find that both *Stipa* and *Aristida*, with their single-flowered spikelets and other advanced characters, represent about the highest stages of development in all these tribes so far dealt with.

The Phalarideae are not so advanced. Though the spikelets are one-flowered they have two extra empty glumes or male flowers below the terminal one and the number of stamens is variable (two, three, four or six). In many respects indeed they are a tribe, which seems to have retained certain primitive features and they are often mountainous in their distribution, e.g. *Ehrharta* in South Africa which connects with *Microlaena* and *Tetrarrhena* in Australia. The genera *Anthoxanthum* and *Hierochloë* extend from the mountains of the tropics to the temperate or frigid zones. Stapf has removed the tribe Oryzeae from the first series of Hackel and has placed it near the Phalarideae. Sometimes in the Oryzeae there are numerous empty glumes and six stamens. The genera are mostly tropical and hygrophilous but *Leersia oryzoides* occurs in north temperate swamps, and *Lygeum spartum* on the high plains of countries bordering the Mediterranean. Both the Oryzeae and the Phalarideae have no close connections with the other tribes.

Hackel's first series consists of tribes which are, on the whole, clearly distinct from those of the second series. Though, floristically, they show a high degree of specialisation yet in some respects they

have retained primitive characters. They have not become widespread in the cold temperate regions, but, on the other hand, they are the most abundant grasses of the moist tropical regions. It would seem that, long after the earlier hygrophilous and mountain types among the bamboos and Festuceae had begun to give rise, by differentiation, to types which were well adapted to colder conditions, and drier conditions, forms were evolved which became dominant in subtropical grassland areas. What the exact origin of the latter has been it is difficult to say. The two main tribes are the Andropogoneae and the Paniceae. The Andropogoneae include some hygrophilous forms, especially in the subtribe Sacchareae, but the majority are of the "bunch grass" type, dominant in mesophytic or somewhat xerophytic tropical and subtropical savannahs and extending into temperate regions. The genus *Andropogon* as defined by Hackel is a very large one now subdivided by Stapf. The grass *Themeda triandra* is dominant over immense areas of grassland in Africa. The Paniceae include hygrophilous genera, e.g. *Setaria* and *Pennisetum*, shade-loving forest forms, e.g. numerous species of *Panicum*, creeping surface-rooting forms, e.g. *Stenotaphrum*, many ruderals, e.g. species of *Panicum*, *Paspalum*, etc. The Paniceae are not so prominent in tropical and subtropical grassland areas. Like some rather highly evolved tropical herbaceous families among the Dicotyledons, e.g. the Acanthaceae, they are most in evidence around forest margins and in hygrophilous situations, playing an entirely subordinate rôle in the vegetation, or they occur as tropical weeds. The tribe Maydeae are a still more specialised small group of tropical or subtropical forms which include the cultivated *Zea mays* and do not call for any special analysis.

Though there are many very primitive grasses in the tropics (as the Bamboos, Arundineae and other Festuceae) the dominant grasses of the subtropical regions are clearly of a rather highly evolved and probably recent phylogenetic type, much more so than the temperate forms. This is quite parallel to what we have learned concerning the evolutionary history of woody types. While the moist, tropical forest areas contain the most ancient types of all, the drier subtropical areas contain many very recent forms, including succulents, etc. The reactions to increasing aridity and especially to desert conditions have apparently taken place at a much later stage than the reactions to cooler or temperate conditions.

ECOLOGICAL DIFFERENTIATION AMONG THE GRASSES

As in the separate families of trees and shrubs so among each of the different tribes of the Gramineae differentiation has proceeded rather far. Even within the limits of a single genus widely different forms have been produced. It is difficult to arrange the different forms in any exact evolutionary series, though, as we have seen, the evidence from phylogeny as regards the characters of the spikelet support the view that, in general, xerophytic types, and types which appear early in the plant succession, ruderal and annual forms, etc., are all highly evolved (e.g. *Aristida*, *Stipa*, *Cynodon*, *Sporobolus*, *Spartina*, etc.). The following classes of forms are ecologically more or less distinct and they represent the final result at the present day of the process of differentiation in this important group but it is not easy to say what the relationships between the different classes have been.

1. Woody types. The Bamboos.
2. The Reed type. Tall-growing forest margin and marsh forms of which the Arundineae are primitive examples, but the same form is adopted by some advanced types among the Paniceae, etc., e.g. *Pennisetum purpureum*, the elephant grass of Africa, and others.
3. Tufted hygrophilous forms with short underground rhizomes. They differ from the Bamboos and Reed Grasses in being much smaller forms.
4. Mesophytic Bunch Grasses (Andropogoneae, etc.).
5. Xerophytic Bunch Grasses (*Aristida*, etc.), a highly evolved type floristically and otherwise. [This ends one line of evolutionary advance.]
6. Sod forming grasses with extravaginal stolons or runners most abundant in temperate regions. Phylogenetically rather primitive forms.
7. Creeping, surface-rooting, and psammophilous forms with long rhizomes. A generally rather heterogeneous class, which have apparently arisen at several different levels of evolutionary development.
8. Climbing grasses and shade-loving scrambling forest species, hygrophilous forest margin stragglers. A few of these are undoubtedly ancient, as among the Bamboos, but the majority are rather highly evolved floristically. The Paniceae include a large number.
9. Annual grasses. These are to be regarded as modern forms

but they have arisen, as in the case of the annual plants, in many widely separated circles of affinity in the different tribes.

THE GENERAL DISTRIBUTION OF GRASSES AND GRASSLANDS

In all the tropical and subtropical areas with increasing aridity forest passes into open "savannah forest" and then into savannah proper, which consists of grassland with scattered trees or patches of forest. Finally there are great areas of grassland without trees. The Campos of Brazil are savannah with low-growing trees isolated like the trees in a grassy orchard. The Llanos of Venezuela are pure grassland with trees, few in number and more or less confined to moister spots. The Pampas of the Argentine are immense areas of more or less pure grassland.

In Africa exactly the same stages are represented—equatorial forest, grassland with forest in the moister areas, open "tree-veld" (savannah) of every possible degree of increasing xerophytism and, once more, great stretches of pure grassland (grassveld). From the north-eastern forest areas of Australia inland towards the dry interior and towards the south, similar gradations are shown.

Over all the great areas of tropical and subtropical grassland the stages of the succession are similar. Pioneer deep-rooted wiry grasses form the early stages, while bunch grasses of a more mesophytic character become dominant in the climax stages. Much of the tropical grassland occurs in forest climatic areas where the true forest stages have been destroyed by fire. The grassy Patanas of Ceylon, the Lalang vegetation of south-eastern Asia, with *Imperata arundinacea* dominant, the elephant grass areas of central Africa with *Pennisetum purpureum*, possibly much of the African grassveld, much of the South American llanos and campos and possibly also some of the eastern prairies of North America are due to a retardation of the natural forest succession or the destruction of climax stages.

The grasslands of temperate regions also cover very large areas in North America, Europe and Asia. In North America, according to Shantz (1924), they may be divided into (1) tall grass (prairie), grassland with bunch grasses (*Andropogon* spp.) and sod grasses (*Stipa* and *Agropyrum*, etc.) nearest the eastern side and most mesophytic, but also occurring on the Pacific side. (2) Short grass (plains), grassland with grama grass (*Bouteloua*), buffalo grass (*Bulbilis*), wire grass (*Aristida*) and also *Agropyrum*, *Stipa*, *Koeleria*, etc., a drier type occurring west of the 100th meridian and east of

the Rockies. (3) Mesquite (desert) grassland with other species of *Bouteloua*, *Hilaria*, *Scleropogon* and *Aristida*, the driest type of all occurring in Texas, New Mexico, Arizona and Mexico.

The steppe regions of Asia and Europe form a vast belt between the northern forests and the central deserts. In many parts the (chernozem) soils are remarkably fertile. The steppe grasses are mostly of the tufted type, species of *Stipa* being dominant with *Koeleria cristata*, *Festuca ovina*, etc. The genus *Stipa* is also most prominent in all the drier steppes, such as occur in Hungary (the pusztas), Roumania and Serbia, and in Spain (the Iberian steppes).

The meadows of temperate countries occur in regions where the precipitation is fairly high and evenly distributed; often no doubt they replace former forests. Meadow grasses belong to the genera *Poa*, *Festuca*, *Agrostis*, *Aira*, *Avena*, *Dactylis*, *Holcus*, *Anthoxanthum*, *Alopecurus*, *Phleum*, *Briza* and others. Many are sod-formers, e.g. *Poa pratensis*, *Festuca rubra*, *Agrostis* spp., etc., yet, on the whole, the tufted forms are even more numerous as regards species. The grasses are all mesophytic.

In mountain regions natural meadows occur in many parts of Europe, Asia and America of different types, either wet or dry. Alpine meadows of the Rockies, for instance, have *Carex* spp. and *Festuca brachyphylla* dominant with a great variety of alpine plants. Some authors would include the eastern prairies as meadow.

Vast though those regions of subtropical and temperate grassland are, they by no means contain all the grasses. As already pointed out in the regions of sclerophyllous vegetation grasses are very numerous though rarely dominant. They are chiefly rather primitive forms, at least floristically, including members of the Festuceae, Aveneae and Hordeae.

The great genus *Danthonia* and its allies are prominent at the Cape and in Australia, while related genera, e.g. *Aira* and *Deschampsia* and *Molinia*, are characteristic of moorland regions in Europe. *Nardus stricta* is a highly evolved northern member of the Hordeae.

The grass-heath or grass-moor type of north temperate grassland has *Nardus stricta*, *Molinia caerulea*, *Deschampsia flexuosa* and *D. caespitosa* with *Agrostis* spp. and *Anthoxanthum odoratum*, etc.

In Britain the "silicious grasslands" (Tansley, 1911), which often replace woodland, have *Nardus* and *Deschampsia flexuosa*, *Agrostis tenuis*, with *Molinia*, the last named in wetter places.

Another class of grass forms which do not, as a rule, enter into the composition of grassland areas are the psammophilous types

occurring on sand dunes and along the seashore. A few seashore grasses are true halophytes, growing in salt or brackish water; the psammophilous creeping forms, which root at the nodes, are efficient sand-binders. Many of this class tend to be very widespread, e.g. *Spartina stricta*, *Sporobolus pungens*, etc. The seashore habitat, like the hygrophilous, is relatively uniform all over the world.

We also have to take into account all the other types of grasses which play a subordinate rôle in vegetation, viz. the climbing forms in forest (e.g. species of *Panicum*, *Olyra latifolia*, *Stipa dregeana*, *Potamophila prehensilis*), the hygrophilous marsh species, some primitive like the Arundineae, others highly developed, the ruderal perennial creeping forms and the annual types. The subordinate grasses of all kinds are undoubtedly mixed in their origin. From the nature of things the earliest grasses must have been subordinate and many ancient forms remain so but the class of subordinate forms, as a whole, has been added to throughout the evolutionary history of the grasses. While a considerable amount of our limited space has been devoted to the question of the origin and differentiation of the grasses and the establishment of grasslands, the importance of this section of our subject clearly justifies it. Nothing else has had a greater influence on the general course of evolutionary history among flowering plants, as well as among the higher animals, than the fact that so much of the total surface of the globe has become completely dominated by this very successful type of plant. It will be necessary now, however, to consider the differentiation of other derivative types of plant form more briefly.

THE GENERAL DIFFERENTIATION OF DERIVATIVE TYPES IN RESPONSE TO COOLER AND DRIER CONDITIONS

Since Raunkiaer's system of classifying the lifeforms of plants is now well known, it is convenient, as far as possible, to refer to his names for the different classes. His classes of Chamaephytes, Hemicryptophytes, Geophytes and Therophytes, arranged in this order (omitting helophytes and hydrophytes) show successive increased responses to adverse conditions and, therefore, to some extent, illustrate an evolutionary sequence. But it should be clearly realised that one class has not necessarily produced the next, though the different classes do grade into one another. Moreover, since the biota has been chiefly concerned in their production we have removed many forest margin Chamaephytes or Cryptophytes and have associated them with Helophytes as representing a primi-

tive class of forms which have not been forced to react to any extent to climatic differentiation.

On the other hand, it cannot be maintained that the Chamaephytes of drier areas have all been derived from forest margin hygrophilous forms. As we have seen, many woody genera of trees and shrubs have by reduction of size, given rise to species which are chamaephytic, geophytic, or even therophytic.

Raunkiaer's class of Nanophanerophytes pass by insensible gradations into the class of Chamaephytes. It may be doubted whether Raunkiaer's "normal spectrum" has been as accurately computed as he believed, though that is a minor point. He assigns only 1 per cent. of the world's flora to the two classes of Hydrophytes and Helophytes combined, which would give a total of about 1440—a figure that seems much too low.

Without applying Raunkiaer's names too rigidly we shall follow his sequence and, where possible, subdivide his classes into certain fairly well defined forms, as follows:

1. Prostrate Chamaephytes. These are either suffruticose or entirely herbaceous. Through the hygrophilous types this class may connect with the straggling lianes. Evolutionary advance here, as elsewhere, has gone hand in hand with increasing xerophytism.

2. Cushion forms. These forms represent a final result of the tendency towards increased branching combined with decrease in size. The cushion-type is sometimes very dense and compact, being rounded or hemispherical in outline. Plants of this type occur in desert or semi-desert regions, in alpine situations and in cold countries. They are commonest at high altitudes on mountain ranges all over the world. One of the most extreme examples is the well-known *Raoulia* (mountain sheep) of New Zealand. Hauri (1912), in a full discussion of the morphology and ecology of cushion plants, distinguishes between (1) typical cushion plants consisting of a single individual with compact texture, (2) cushion-like dwarf shrubs which are less compact and (3) cushions formed of several distinct plants of the same or different species.

3. Herbaceous succulents. The physiological significance of the succulent habit has already been discussed in connection with trees and shrubs, but there are altogether relatively few woody succulents. The vast majority are herbaceous or, at most, suffruticose. Such smaller forms are completely dominant over great stretches of the South African Karroo and they are common in similar dry regions elsewhere. The fact that they are, as a rule, highly evolved

floristically is very striking, especially such forms as *Mesembryanthemum*, *Euphorbia*, the *Stapeliae*, etc. Halophytes are also generally more or less succulent and include many rather specialised herbaceous forms in different circles of affinity. Other succulents are found in rocky places, in waste places as ruderals, and in various open situations.

Other well-defined forms occur among the Hemicryptophytes and intermediate types.

4. Rosette (or half-rosette) plants. This type is brought about by a shortening of the internodes and a consequent crowding of the leaves. In addition to increased protection various other advantages are supposed to accrue, e.g. the obtaining of heat from the soil and the utilising of dew deposited at night. Rosette forms are common in a great variety of situations showing all gradations from the mesophytic to the xerophytic. They occur in hygrophilous marsh and forest margin situations throughout the grassland areas, in waste places and open situations of all kinds and in semi-desert and desert regions. On the whole they are commoner at high altitudes than at lower and Bonnier showed that some species, which at low altitudes have long internodes, produce rosette forms in alpine situations. The rosette form is often combined with succulence and often also with the next class.

5. Plants with woody "rootstocks." This is a very common type in grassland areas. The aerial parts are herbaceous or very slightly woody and die back each year (or they frequently are burned off) leaving an underground woody stem or "xylopodium" as it has been called by Lindman (1900). The renewal buds are just below the soil surface, as a rule, but they are very irregularly placed, and the general form of the aerial growth of branches varies considerably. Sometimes it is tufted or caespitose, sometimes straggling or, if the underground rhizome itself tends to spread, the class becomes transitional to the travelling geophytes which, however, are further distinguished by their rhizomes and renewal buds being more deeply buried in the soil. This class in the other direction, as already explained, connect fairly obviously with the phanerophytes.

6. Travelling geophytes. These have horizontally placed underground rhizomes, which give rise either to aerial foliage leaves or to erect epigeal shoots which bear leaves. As we have seen, they are common among the forms occurring around forest margins and in marshy situations and are, therefore, to be reckoned rather primitive in their origins. They may even connect with the lianes,

epiphytes and stragglers of the forest undergrowth. In a word the biota has been largely concerned in their production apart altogether from increasing climatic differentiation, a fact which illustrates once more how Raunkiaer's system tends to fail as a phylogenetic system of classifying lifeforms. Travelling geophytes also are common as psammophytes on sand dunes and as perennial weeds in cultivated land.

7. Mat-geophytes. These are the so-called bulbous plants, though the storage organs may be stem tubers (or corms) or root tubers, as well as true bulbs. They are stationary forms, feebly-branched, and have renewal buds well protected. Though numerous Dicotyledons are geophytic the majority are monocotyledonous, especially the Liliaceae, Amaryllidaceae, Iridaceae and Orchidaceae. Several of the genera in these families are very large and widespread (e.g. *Allium* (300 sp.), *Scilla* (100 sp.), *Ornithogalum* (90 sp.), *Lilium* (50 sp.), *Tulipa* (50 sp.), *Hypoxis* (60 sp.), *Iris* (125 sp.), *Moraea* (60 sp.), *Gladiolus* (150 sp.), *Crocus* (60 sp.)). Raunkiaer's estimate of 3 per cent. of geophytes for the whole world's flora, which would give a total of 4300, is again probably too low. I have estimated the total for Natal as 18 per cent. (Bews, 1916). Though geophytes have probably had very ancient origins, much of their differentiation has been relatively recent. They are especially abundant in drier subtropical and temperate grassland areas.

More attention should be given to their physiological behaviour. While in some, probably the more recent types, new storage organs are formed annually, in others the storage organs are perennial and may go on enlarging year after year. In the drier subtropical areas water as well as food material is stored underground by geophytes. Their renewal of growth in spring is then determined largely by rise in temperature rather than by the incidence of the first rains.

In general they flower in spring, often before they renew their foliage, and recommence the work of assimilation. In many cases the formation of tubers is known to be intimately bound up with infection by fungi, and a general fungal theory of tuberisation is favoured by many (see Bernard, 1902, 1909; Coulter, Barnes and Cowles, 1911; Magrou, 1921).

8. Therophytes. Annual plants, though they have been produced in very widely diverse circles of affinity, are to be generally regarded as the most recent of all forms. Under natural conditions they are particularly characteristic of the most adverse regions and situations (deserts and open xerophytic habitats). A high pro-

portion of all desert floras consists of short-lived ephemerals, which spring up after the infrequent rains, pass through their whole vegetative life in the course of a few weeks, flower, form seed and die. The angiospermous seed in its most highly evolved form, with hard resistant seed coats and long viability, is the most efficient organ of all in resisting adverse conditions. Annuals are also peculiarly suited to the types of habitat which have resulted from man's interference and they are abundant as weeds in cultivated land or as ruderals generally in waste places. Many such types have become very widespread as a result of man's activities.

The physiological processes of annual plants, though most fully investigated and best known, since such plants can be most easily and quickly grown for experimental purposes, are of a somewhat specialised character, like the plants themselves. Annuals do not in their vegetative life react in the same way as perennials. They do not store food except in their seeds and until they begin seed production their growth follows Blackman's *Law of Compound Interest* (1919). They are thoroughly efficient assimilating machines, they expand their total leaf area as much as possible so as ultimately to produce seed as efficiently as possible, but their whole life-cycle differs from perennial forms where storage takes place in vegetative organs. Biennials are related to annuals. During their first season, most biennials develop a rosette of leaves and store up food. In their second season an erect shoot is formed which bears flowers and forms seeds. The biennials are characteristic of cold temperate countries.

HABITAT FORMS

While the life-forms of plants always bear a certain definite relationship to the habitats where they occur, yet the origin of the different forms has been due, partly at least, to internal forces which are entirely independent of the environment. Views still differ as to the exact relationship of the internal and external forces influencing evolutionary differentiation. Some believe that the environment does nothing more than sort out the material supplied through the agency of the independent forces, which result in variations great or small. Others are more inclined to think that the external environment may not only use the material already supplied, by selecting the types best suited to its varying requirements, but may exercise a guiding influence over its actual production, that it may lead directly to permanent changes in the basic hereditary developmental processes, and not merely deal with the results of

processes over which it has no controlling influence. The recent work of Harrison and Garrett (1926) on the induction of Melanism in the Lepidoptera, and its subsequent inheritance supplies definite proof that environmental influence can be brought to bear, powerful enough to influence the germ plasm of animals. As far as plants are concerned botanists have always been more inclined than zoologists to adopt the Neo-Lamarckian standpoint.

But in dealing with the facts of distribution and of ecological differentiation in general we have begun at the other end of the scale. We have taken the great main classes of plant forms and have tried to analyse the history of their phylogenetic differentiation. When we come down to more minute differences, such as are exhibited within the limits of a species, the relationship of our subject to modern ideas in genetics, becomes more obvious. Turesson in various recent papers (1922-5) has endeavoured to show that the mass of genetically different biotypes, which make up the Linnean species do not distribute themselves indiscriminately over an area comprising different types of localities. The biotypes, on the contrary, are found in nature to be grouped into different types each confined to a definite habitat. The Linnean species from the standpoint of "genecology" Turesson designates the "ecospecies." The habitat types he terms "ecotypes" and he looks upon them as the products that have arisen through the sorting and controlling effect of the habitat factors upon the heterogeneous species population. The ecotypes are *genotypal* responses of an ecospecies to particular habitats, as Turesson claims to have shown by cultural experiments. One and the same ecospecies thus succeeds in populating widely different habitats. On the other hand, phenotypical reactions may result in the production of reaction types which are due entirely to the modificatory influence of the environmental factors. These are called "ecophenes" by Turesson. Whether this distinction between ecophenes and ecotypes is quite so definite and necessary as Turesson believes or may not be due merely to a lack of fixation in the former, there can be no doubt that the numerous facts recorded for the different species dealt with are extremely valuable. In his latest paper Turesson has shown that a differentiation of parallel ecotypes takes place within different species, a fact which makes a uniform system of naming possible. The following ecotypic names are proposed: *oecotypus campestris*, *oect. arenarius*, *oect. salinus*, *oect. sub-alpinus*, *oect. alpinus* and numerous ecotypes of different species investigated are placed in their respective groups. While Turesson's

names are very convenient as applied to habitat forms within the Linnean species (ecotypes of the ecospecies) the term "habitat form" has been applied in a wider sense to the distinct species which have reacted in definite ways to distinctive habitats.

Thus Warming has distinguished the main classes, hydrophytes, mesophytes, halophytes, xerophytes, as well as (in his later work) helophytes, oxylophytes, psychrophytes, psammophytes, chersophytes, psilophytes, lithophytes and eremophytes. In such a classification of plant forms the "life-form" concept is, to a large extent, abandoned, and emphasis is laid wholly on the habitat. It follows from what has been shown in all the preceding chapters that, in a very general way, some of these habitat forms are more ancient than others. Xerophytism is a general evolutionary trend and xerophytes are, as a rule, derivative, as are hydrophytes in another direction. The ancient unchanging types of habitat, it may be repeated, are more likely to contain ancient forms than modern types of habitat. But it has also been shown that previous writers have not laid sufficient emphasis on the effects of the biota. There are hosts of derivative types even among the mesophytic or hygrophilous plants of tropical rain-forest, i.e. among those that occupy subordinate positions in that ancient plant community.

It may be well, however, in conclusion, to examine very briefly a few habitat forms (using the term in the wider sense), which have not been sufficiently dealt with already.

1. **Halophytes.** Saline soils occur near the seashore, near salt springs and salt lakes and in dry steppe or desert regions. The halophytic flora is, on the whole, a poor one, but various families have a few or many halophytic genera or species, e.g. Chenopodiaceae, Tamaricaceae, Frankeniaceae, Aizoaceae, Plumbaginaceae, Portulacaceae, Zygophyllaceae, Cruciferae, Helobieae, Cyperaceae, Gramineae, etc. The prevalent succulence of halophytes is largely a direct response to the salinity of the habitat since halophytes commonly lose much of their succulence when grown in soils poor in sodium chloride. Other of their characters are more definitely fixed. Along the seashore many halophytes are very widespread, e.g. *Ipomoea pes-caprae*, species of *Canavalia*, *Salicornia*, *Suaeda*, *Atriplex*, *Sporobolus*, *Spartina*, *Triglochin*, etc. Inland, in salt pans, salt deserts, etc., species of *Suaeda*, *Salicornia*, *Salsola*, *Frankenia*, *Tamarix*, *Statice* are most characteristic and widespread.

2. **Psammophytes.** The soil in this case is immature and usually sterile and all the vegetation more or less xerophytic. Long creeping

rhizomes or very deep roots are the characteristic feature of psammophytes. With advance in the plant succession shrubs and then trees take possession and the sand becomes definitely fixed with resulting changes in the soil conditions. In Europe, dune heath with *Empetrum*, *Calluna*, etc., or dune bushland with *Hippophaë*, etc., or finally pine forest, as on the Baltic coasts, represent successive stages. Similarly in the sclerophyllous regions Macchia is the climax stage, in North America poplars, willows, or coniferous forest, in Asia species of *Pinus*, *Betula*, *Populus*, *Salix* and *Ulmus*. In tropical and subtropical regions psammophilous scrub or forest include a variety of species, in which the family Sapotaceae (*Mimusops*, *Sideroxylon*, etc.) are often rather prominent or in wetter types, *Barringtonia racemosa*, *Hibiscus tiliaceus*, etc., are very widespread. In Brazil the littoral forest on sandy soil is known as "restinga."

3. Psychrophytes, or plants of very cold habitats, are a still more heterogeneous group occurring in subglacial areas on high mountains or in the circumpolar regions. They are dwarf shrubs, suffrutices or herbs. Nanism is the prevailing characteristic in all the species, both in the plants as a whole and in their separate organs. Leaves are small, internodes short, or if the shoots are elongated then they are prostrate. Cushion plants, rosette forms and tufted forms are common. Ethereal oils, anthocyan pigments, etc., are sometimes a feature.

4. Other habitat forms of Warming may be passed over with very brief reference. Lithophytes proper (rock surface plants) consist mostly of lower forms of plant life. Chomophytes (Chasmophytes) or rock crevice plants have few special characteristics and usually include samples of any plants occurring in the neighbourhood. The Chersophytes or plants of waste land are highly evolved, often annual types, but they have already been sufficiently dealt with, as have also the Mesophytes, sclerophyllous plants and Psilophytes (grassland plants). Warming's class of Oxylophytes (plants of sour soils) is the least satisfactory of all these habitat forms. Their general distribution and physiognomy probably depend on climate, and the sourness of the soil is a *result* of the combined effects of climate and vegetation and is not the *cause* of responses. We have already discussed the connections of moorland plants and the more ancient mountain sclerophyllous types.

5. The Tundra vegetation Warming includes among his moorland oxylophytic types. It covers great areas in the northern parts of Europe, Asia and America. The soil is wet and the air moist but the

low temperature checks absorption. The landscape is monotonous, desolate and treeless. Two types are distinguished, the moss-tundra and the lichen-tundra—the former moist, the latter dry. The moss-tundra consists of mosses with dwarf shrubs including *Empetrum*, *Betula nana* and *Vaccinium myrtillus* and small herbs with often brilliantly coloured flowers, which in places are rather abundant. In the lichen-tundra, a thick carpet of fruticose lichens (*Cladonia*, etc.) gives the landscape a characteristic yellow-grey colour. Between the lichens are found *Empetrum*, *Betula nana*, *Loiseluria procumbens*, *Calluna*, *Juniperus communis* and other dwarf shrubs, *Nardus stricta*, *Deschampsia flexuosa* and herbs, e.g. *Hieracium* spp. The tundra vegetation obviously connects with the moorland and through that with sclerophyllous vegetation. Its chief interest is that it represents the most impoverished and most extreme type of response to cold conditions.

6. Desert plants. Warming includes both desert and steppe plants in his *eremophytes*, though steppe plants in general should rather be classed with *psilophytes* even though the drier types of steppe do grade into deserts. It is true that the term "desert" is used rather vaguely by different authors so as to include any fairly dry region, e.g. the South African Karroo and other "shrub steppes." The best test of real desert conditions from the vegetation standpoint is a very high proportion of annuals. In true desert the individual perennials are few and far apart. They are universally of the most extreme class of xerophytes, usually either succulent or thorny or often both. The annuals often tend to cluster round the scattered bushes of perennials so that even in desert there is a kind of plant succession, which, however, is the reverse of the usual order. Desert plants represent the final result of specialisation in response to increased aridity.

SUMMARY

1. Among all the responses shown by Angiosperms to climatic differentiation in many ways the most important has been the evolution of the grasses—a type which has been successful in assuming complete dominance over vast areas of the world's surface. An attempt has, therefore, been made to analyse the floristic and ecological differentiation of the grasses in some detail.

The bamboos are regarded as the most primitive and they are tropical in distribution, but have produced some herbaceous forms on the mountains of South America, which suggest a possible origin for the *Festuceae* and *Aveneae*, tribes which, on floristic grounds, are

regarded as the most primitive of the ordinary grasses. The subtribe Arundineae remain mostly hygrophilous and tropical. Even within the limits of the Festuceae, however, forms have been evolved to suit most modern climatic conditions. The same applies to the Aveneae and Hordeae. Connections are shown in all these tribes between the mountain types of the southern hemisphere and tropics and the Mediterranean region and moorland grasses of the northern hemisphere. The Chlorideae are a more advanced tribe and the Agrostideae have reached a high evolutionary level in the subtribe Stipeae which include *Stipa* and *Aristida*, the former the chief type in steppe regions and the latter in drier subtropical regions. The Phalarideae and Oryzeae are not apparently closely connected with other tribes, and in some respects have retained primitive characters, but again show specialisation in various directions. The tropical and subtropical grasses belong mostly to the tribes Andropogoneae and Paniceae, the former being dominant over large areas of subtropical grassland, the latter more subordinate types around forest margins in moist places and as weeds. All these tropical and subtropical grasses are rather highly evolved as are most derivative types of woody plants in the drier tropical and subtropical regions.

2. Ecologically the grasses have become differentiated to give (1) woody types, (2) the reed type (both rather primitive), (3) tufted hygrophilous forms, (4) mesophytic bunch grasses, (5) xerophytic bunch grasses (along one line of response), (6) sod-forming grasses, (7) creeping, surface-rooting and psammophilous forms, (8) climbing grasses and shade-loving scramblers, (9) annual grasses. The last mentioned are probably usually recent types but the interconnections between the other forms are rather uncertain. In each tribe and in much narrower circles of affinity, even within the limits of the larger genera, a variety of very distinct forms commonly occur.

3. An account of the general distribution of the grasses and grasslands of the world is given but it can hardly be condensed any further in this summary.

4. In classifying other derivative types which have responded to drier and cooler conditions Raunkiaer's sequence of arrangement is followed, but it is modified somewhat since the different classes of derivative plant form have had diverse points of origin. The following fairly well defined types are described: (1) Prostrate chamaephytes, (2) Cushion forms, (3) Herbaceous succulents, (4) Rosette plants, (5) Plants with woody rootstocks, (6) Travelling geophytes, (7) Mat-geophytes, (8) Therophytes.

5. In connection with "habitat forms" Turesson's recent work is discussed with reference to the differentiation of the Linnean species (ecospecies) into various habitat forms (or ecotypes). In a wider sense classes of "habitat forms" have been recognised by Warming and others made up of different species which have reacted in a similar way. Most of these, e.g. xerophytes, mesophytes, helophytes, hydrophytes, etc., have been sufficiently described in earlier chapters but a few notes are added on halophytes, psammophytes, psychrophytes, tundra vegetation and desert plants.

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(Concluded)

THE BEHAVIOUR OF THE CYANOGENETIC GLUCOSIDES OF CHERRY LAUREL DURING STARVATION

By H. GODWIN AND L. R. BISHOP

From the Botany School, Cambridge

(With 15 Graphs in the Text)

THE study of the various aspects of the problem of starvation respiration and yellowing in leaves of cherry laurel (*Prunus Laurocerasus*) brought into prominence the behaviour of the cyano-genetic glucosides which they contain. These compounds represent a fairly large fraction of the stored carbohydrate in the leaves. The present paper contains an account of the methods employed in a study of the relations of the glucosides to the yellowing and respiration phenomena of starvation; it gives the results obtained, and concludes with a consideration of glucoside behaviour from the standpoint of a general hypothesis of the metabolism of the starving leaf.

BEHAVIOUR OF HCN DURING STARVATION

Previous workers established the following points. Treub¹ has shown that with several different species of leaf the HCN diminishes with age and disappears at the time of fall and also disappears during the yellowing of detached leaves. Guignard² found two exceptions to this in *Sambucus nigra* and *Indigofera galeoides* where the HCN content remains unaltered at leaf-fall. One of us (H. G.) has already shown (Ph.D. thesis, Cambridge University Library) that in cherry laurel also, the HCN content decreases during yellowing and in the fully yellowed leaf there is no HCN. This loss was found to take place if the leaf yellowed off or on the tree, in the light or in the dark.

BEHAVIOUR OF CHERRY-LAUREL LEAVES IN YELLOWING AND RESPIRATION

The form of the respiration curve for mature cherry laurel leaves when starved has been described by Dr F. F. Blackman³.

¹ *Ann. du Jard. Bot. de Buitenzorg*, 21, 1907.

² *C. R. Acad. des Sciences*, 141, 1905, 143, 1906, 147, 1908.

³ *Report of Br. Assoc.* 1908, and University Lectures.

The respiration rate plotted against starvation-time shows an initial fall to a low value in all cases. Subsequently the curve rises to a hump, the apex of which occurs approximately at the stage of 50 per cent. yellowing in the leaf. From this apex the curve falls away again to a low value, until the onset of browning and fungal and bacterial attack causes a last rapid rise.

This course of the respiration with starvation of the leaves however only represents the sequence in mature leaves. One of us has shown (H. G.) that the behaviour of leaves during starvation varies with their age from unfolding upon the tree. In leaves of all ages the initial fall of the respiration rate to a low value occurs. Young leaves (1-2 months from unfolding) show no hump and do not yellow. Browning and general disintegration commence at the same time as the final rise in the respiration. With leaves about three months old the first signs of a hump can be detected and the commencement of yellowing is contemporaneous with this. The yellowing is overtaken by the final browning, and the corresponding final increase in the respiration. With increasing age from unfolding a corresponding increase in size of the respiration hump is found and in leaves 20 months old the peak rises as high as the initial value from which the respiration first falls. The onset of browning and fungus development and the final rise in respiration are correspondingly delayed.

EXPERIMENTAL METHOD

The leaves used in all the experiments came from the same bush.

The hydrocyanic acid content of the leaves was measured by the method described by one of us (L. R. B.)¹. The reasons given in that paper for regarding the HCN as a true measure of the cyano-genetic glucoside content of the leaf were regarded as sufficient to justify the acceptance of this assumption here.

The attitude adopted in this paper is to regard the stored glucoside as a necessary result of the upgrade metabolism of the cherry laurel plant, and not as an intended protective compound or definite food reserve. When the glucoside is split it seems reasonable to suppose that the liberated sugar is used, like any other, in respiration. Hence we have calculated the respiratory CO_2 equivalent to the HCN measured, assuming all the glucoside to be in the form of prulaurasin, and all the glucose of the prulaurasin to be fully oxidised.

The rate curves for glucoside loss and yellowing which are given are derived from smoothed percentage content curves, and in conse-

¹ *Bio. Journal*, 1927.

quence have no very exact quantitative significance; but, however the smoothing curves are drawn, the resulting variations in size and form of the rate curves are not sufficient to affect the deductions drawn from them in this paper.

Experiment 1. Whole leaves, 21 months old. Started February 13th.

Leaves 21 months from bud opening.

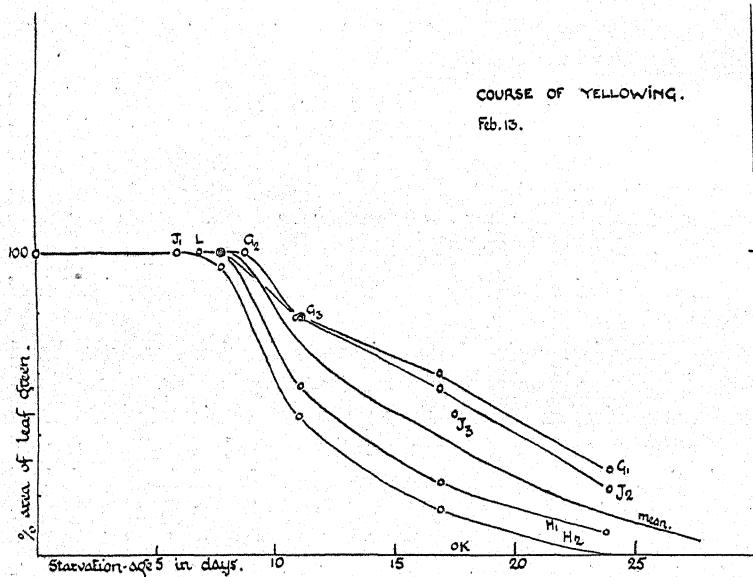
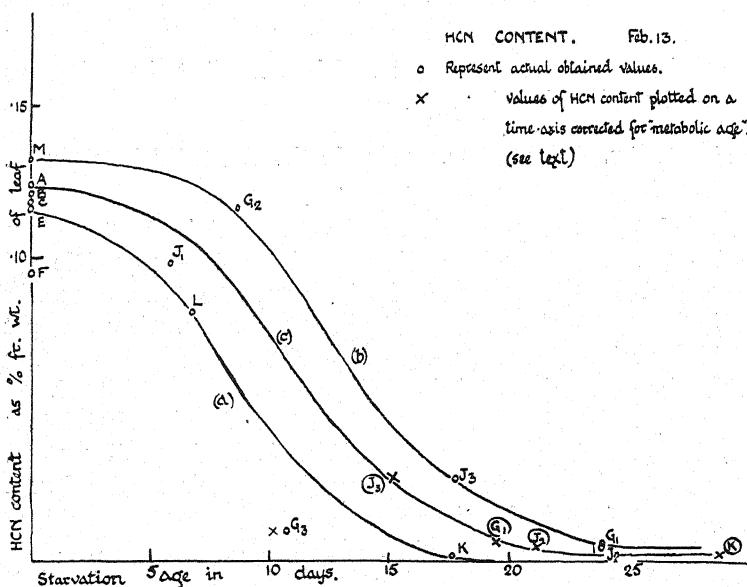
The leaves were gathered from a mature bush in the Cambridge Botanic Garden. They were selected to be as alike as possible and were marked with a letter indicating the branch, and a number indicating their position from the top of the branch. They were put with the petioles in water and were brought to the laboratory where the surface was quickly dried and they were separately weighed.

(a) *Initial HCN content.* One whole leaf *M* and six half leaves (*A*, *B*, *C*, *D*, *E*, *F*) were analysed immediately for HCN content, and the result here and throughout the paper is expressed as a percentage of the fresh weight.

(b) *Alteration of HCN content.* Six whole leaves (*G*₂, *G*₃, *J*₁, *J*₃, *K* and *L*) were sealed in another light-proof receptacle with their petioles in water and were kept in a water bath alongside the respiration set. A current of air was maintained over them but the respiration was not measured. After varying periods single leaves were taken out and drawn (for planimetry) and analysed to determine the HCN content.

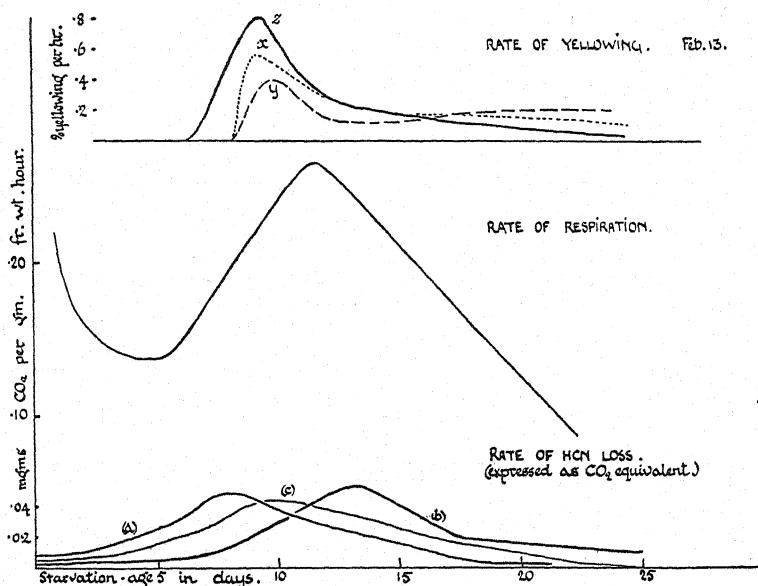
(c) *Respiration.* Four leaves (*H*₁, *H*₂, *G*₁, *J*₂) were placed with their petioles in water in a sealed light-proof container which was immersed in a water-bath maintained at 20.8° C. A slow stream of CO₂-free air was maintained through the chamber and passed on through baryta solution in "Petenkoffer" tubes. By titration of the baryta solution at intervals of 16 or 24 hours a continuous record was obtained of the CO₂ output formed in the respiration of this sample set of leaves.

(d) *Yellowing.* From time to time the chamber was opened and an estimation made by eye of the extent of yellowing. The estimation was carried out by eye since previous experiments had shown that pressure and handling upset the normal smooth course of respiration. The respiratory measurements lasted for a period of 558 hours and at the end of that time the leaves *J*₁ and *G*₂ were taken out and careful actual size drawings were made of the whole leaf and the yellowed areas. These drawings were subsequently planimetered. After drawing the leaves were analysed for HCN content.



The result of these measurements, during the progressive starvation of the leaves, was a series of values for yellowing, HCN content and respiration.

These values have been plotted as points in the Graphs 1 and 2 for HCN content and yellowing respectively. The very regular values for the rate of carbon dioxide output have been given as a smoothed curve in Graph 3.



Graph 3

CONSIDERATION OF THE DATA

The rather widely scattered points on the HCN graph, though demonstrating the progressive diminution in the HCN content with time, do not fall on any single curve, though they may be seen to be distributed about a sigmoid curve. In the light of the later experiments in which a much larger number of points were obtained (e.g. Experiment 3, Graph 9) we have thought it best to include all the points in a broad band limited by two sigmoid curves, and a median line has been added. The data for yellowing have more coherence since for four of the leaves eye estimations at successive times were made on the same leaf so that time progress curves have been drawn. The additional single points, G_2 , G_3 , J_1 , J_3 , K and L ,

given by the leaves about to be analysed fall in line with these first drawn curves. These progress curves are also of the sigmoid type and here also a median curve for yellowing has been added.

The respiration curve given in the middle of Graph 3 is, of course, a rate curve and the data of yellowing and HCN loss have therefore been converted into rate curves also for purposes of comparison. The glucoside loss is given assuming that all the HCN is combined in the form of prulaurasin and the sugar molecule of this has been utilised in respiration. This equivalent CO_2 has been given as mg. per gm. fresh weight per hour, which is on the same scale as the respiration graph so that the two curves are comparable. The three curves a , b , c showing HCN content in Graph 1 have all been expressed as rate curves of HCN loss in Graph 3.

The median and limiting curves for percentage yellowing have also been translated into rate curves and are expressed in terms of percentage yellowing per hour (x , y and z , Graph 3).

The results show the following main points:

- (1) During starvation cyanogenetic glucoside disappears.
- (2) The loss begins in early stages and probably before any yellowing can be seen.
- (3) The end of yellowing shows leaves entirely depleted of glucoside.
- (4) The rate of glucoside loss increases after a time to a maximum and then decreases.
- (5) The period of maximum loss of HCN appears to coincide fairly closely in time with similar maxima in the rates of CO_2 output and of yellowing.

THE CONCEPTION OF "METABOLIC AGE"

The closeness of the connection between CO_2 output, yellowing and glucoside loss in time of origin, maximum development and diminution, must be regarded as evidence that all three are manifestations of an underlying metabolic breakdown of the senescent leaf. If these three are closely correlated then the grade of any one of them should give a measure of what may be termed the "metabolic age" of the leaf. The degree of yellowing of the leaf may be determined by inspection and so affords the simplest measure of this metabolic age. Leaves which yellow more rapidly than those following the mean curve of yellowing will be at all times of greater metabolic age than the average leaf, and those yellowing more slowly of lesser metabolic age. Thus it will be seen that in Graph 2, J_3

may be spoken of as being $2\frac{1}{2}$ days behind the mean curve and leaves H_1 and H_2 are both ahead of the mean curve.

Leaves which are "young" in respect of yellowing should be also "young" in respect of rate of glucoside loss. Reference to Graphs 1 and 2 will show that this is the case. For instance, J_3 is "young" judged by both standards while K is old by both standards. (G_3 is the only exceptional case found in our data: the HCN estimation is presumed to be wrong.) The crosses shown in Graph 1 are the values of HCN content of the leaves J_3 , G_2 , J_2 and K , when plotted on the time scale at distances derived by a correction for metabolic age as revealed by the yellowing graph. It is striking how good a mean curve these points make in the HCN graph, and the result suggests that any leaf would be judged to have the same metabolic age either from its yellowing behaviour or its HCN losses. This seems to indicate that the relation between the rates of yellowing and of HCN loss is extremely intimate.

LOSS OF HCN IN THE GREEN AND YELLOW PARTS

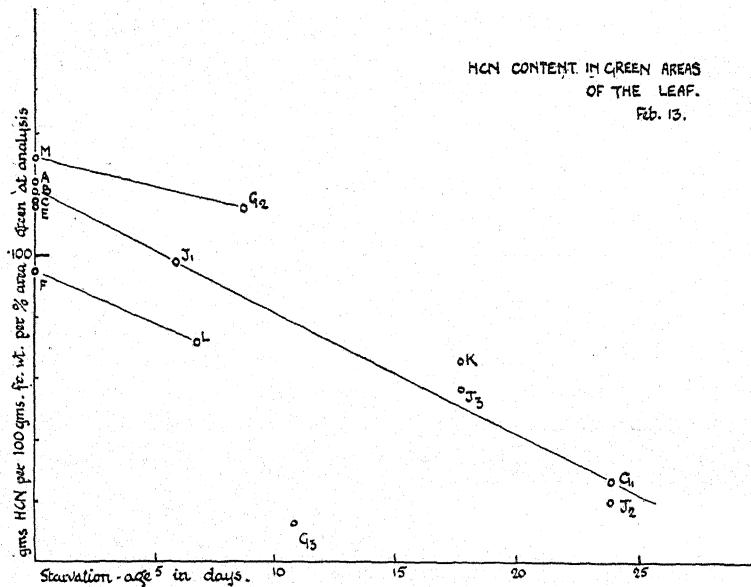
By comparing Graph 1 and Graph 2 it will be seen that very probably some loss of HCN occurred before yellowing set in. Hence it became desirable to know if this loss was due merely to incipient yellowing or to losses in the normal metabolism of the starving green parts. In later experiments the latter alternative was confirmed by more detailed observations over the initial period. In this and other experiments evidence on this point was obtained by calculation. Previous experiments had shown that completely yellowed leaves or parts of leaves are completely devoid of HCN. Thus to separate the two processes the HCN has been calculated assuming all the HCN to be in the green parts. It has been expressed as the following quantity

$$\frac{\text{HCN content}}{\text{fresh weight}} \times \frac{100}{\% \text{ greenness}} \text{ in Graph 4.}$$

This clearly shows that there was a steady decline to a very low HCN content taking place in the green parts (G_3 is again aberrant). We may picture the HCN content as steadily declining in every cell of the leaf which remains green, and as being very rapidly lowered as the cells turn yellow. This seems the most plausible way of explaining at once the steady slow rate of HCN loss in the green areas of the leaf and the sudden rise in the rate of HCN loss which coincides with the time of most rapid yellowing.

RELATION OF THE AMOUNTS OF HCN LOSS AND CO₂ OUTPUT

By comparing the two rate curves of CO₂ output in the respiration and that calculated as coming from the glucoside sugar, it will be seen (a) that the quantity evolved from the slow HCN loss is small in comparison with the total evolved during this first period; (b) the CO₂ arising from the sugar liberated in the rapid HCN loss would be a much larger amount, but this would still not be sufficient to account for all the *extra* CO₂ of the respiration hump. This is



Graph 4

consistent with evidence from other sources that at the same time (unpublished data—Hon. Mrs Onslow and A. R. Clapham) starch also is rapidly broken down. This failure to account for all the extra CO₂ would still hold if even a large part of the HCN were in the form of a *di*-glucoside such as amygdalin, i.e. with two molecules of sugar per molecule of HCN.

Experiment 2. Half-leaves, 21 months old. Started February 13th.

The wide scatter in initial contents of HCN led to this attempt to get a more accurate measure of the loss by the half-leaf method. The leaves were comparable in age and treatment with those in the

last experiment except for the halving. Each leaf was cut exactly down the centre of the mid-rib and both halves were weighed. Preliminary experiments had shown that the two halves of the leaf did not differ significantly in HCN content and that detached halves showed the same type of yellowing as detached whole leaves. One-half of each leaf was analysed immediately and the remaining half-leaves were put together and treated in exactly the same manner as the stock set of leaves in the last experiment.

In Graph 5 the HCN values for the starved halves are expressed as percentages of the content of the corresponding halves analysed at the beginning of the experiment. This is justifiable since it was found that corresponding halves do not differ more than 1-2 per cent. in their HCN content expressed as a percentage of the fresh weight.

In its general characters Graph 5 agrees with the corresponding graph in the first experiment (Graph 1), but the scatter of the points has been reduced remarkably, thus strengthening the earlier conclusions drawn in Experiment 1 as to the shape of this curve.

It is noticeable that up to 100 hours no appreciable loss of HCN occurs, in spite of the injury and exposed surfaces.

The yellowing curve in Graph 6 shows great regularity.

It is only possible to explain this regularity in HCN loss and yellowing by supposing that the wounding reduces to a similar state leaves initially variable.

Twelve half-leaves were used in a respiration experiment.

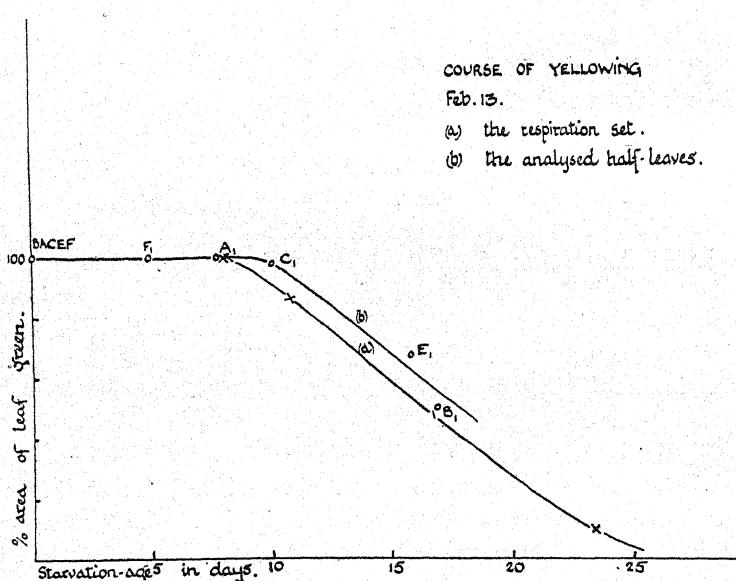
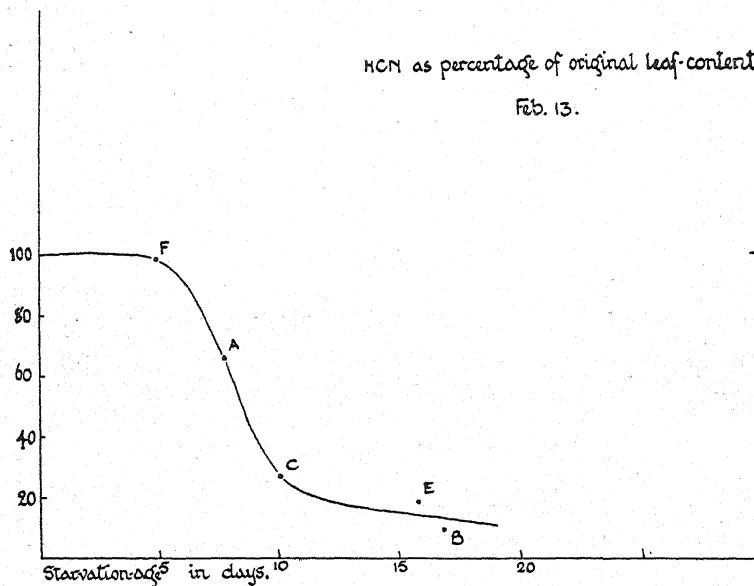
Graph 7 shows how closely the respiration of the half-leaves follows that of the whole leaves.

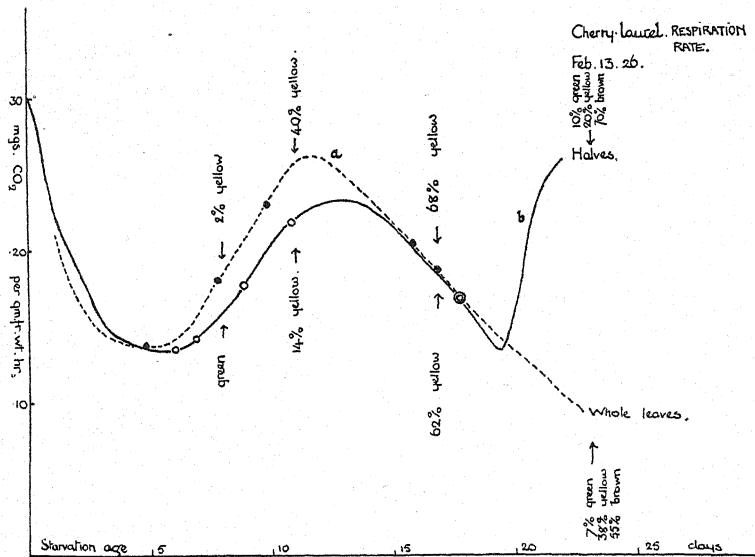
In Graph 8 are shown the rate curves for yellowing (*b*), CO_2 equivalent to the glucoside loss (*a*) and respiration (*r*).

It will be seen that this experiment bears out the conclusions given in Experiment 1. The incidence of yellowing and HCN loss coincide as closely as in Experiment 1 but differ more in duration. There is no evidence of an initial slow loss of HCN.

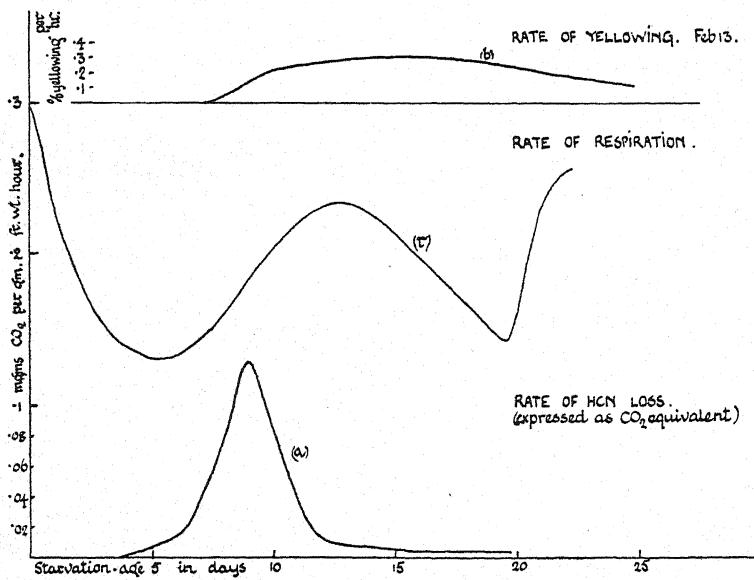
Experiment 3. Whole leaves, 2½ months old. Started July 10th.

Nine sets of three leaves were used as a stock and one set of four leaves was used as a measure of the respiration. The treatment was exactly the same as in Experiment 1, except that on each occasion on which the stock was opened a set of *three* leaves was taken out. The experiment lasted 780 hours.





Graph 7



Graph 8

Graph 9 shows the change of HCN content with time and Graph 10 the corresponding behaviour in yellowing. The rate curves derived from the smoothed total curves are given on Graph 11 with the respiration rate.

The HCN curve is very similar to that of Graph 1, but the scatter of the points is within a narrower band, so that the sigmoid curve is here shown much more clearly.

The extreme youth of the leaves is manifest in the associated phenomena of yellowing, respiration hump, and rapid HCN loss, all of which appear very late.

Also by reason of this youthfulness these phenomena of senescence are all only slightly developed and so the data need not be analysed further.

It may be noticed that in Graph 9 the metabolic ageing of all leaves from the same branch is similar. Thus all the leaves from Branch *B* age rapidly, i.e. they lie on the lower curve of HCN content, whereas those from branch *H* age slowly. This emphasises the fact that the band is not produced by the simple scatter of individuals, but embraces a number of parallel and independent metabolic courses. Both the limits and the mean thus probably represent the actual courses followed by the individual leaves.

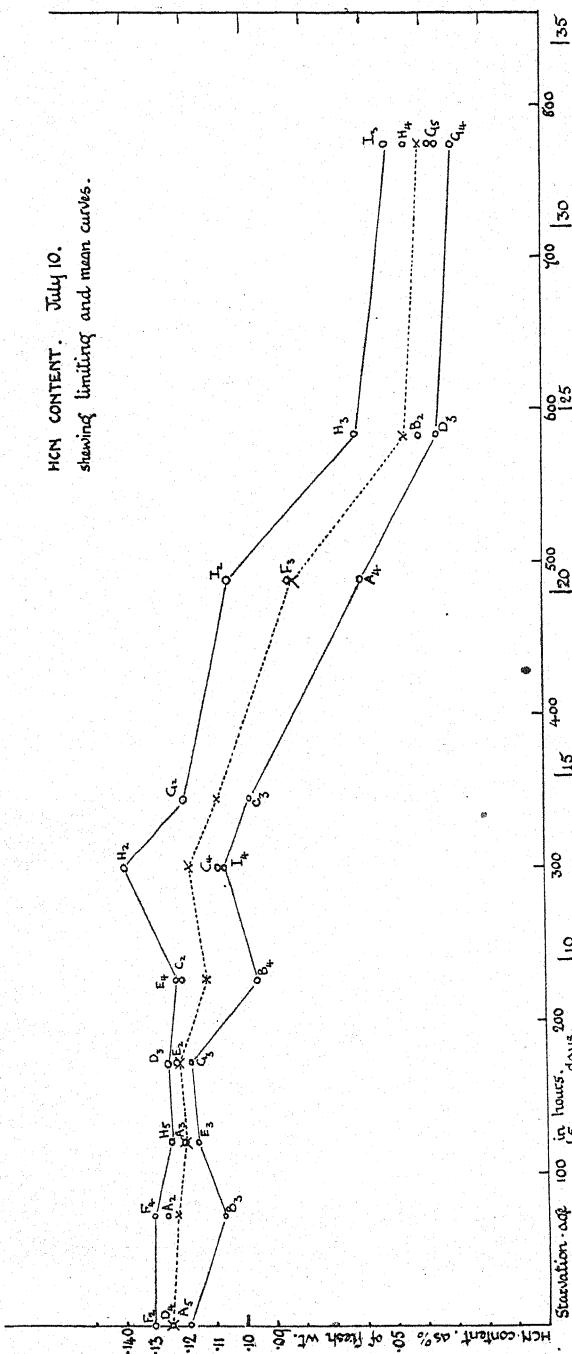
Experiment 4. Leaves 13 months old. Started June 3rd.

This experiment was carried out on the same lines as Experiment 1 but was much more detailed.

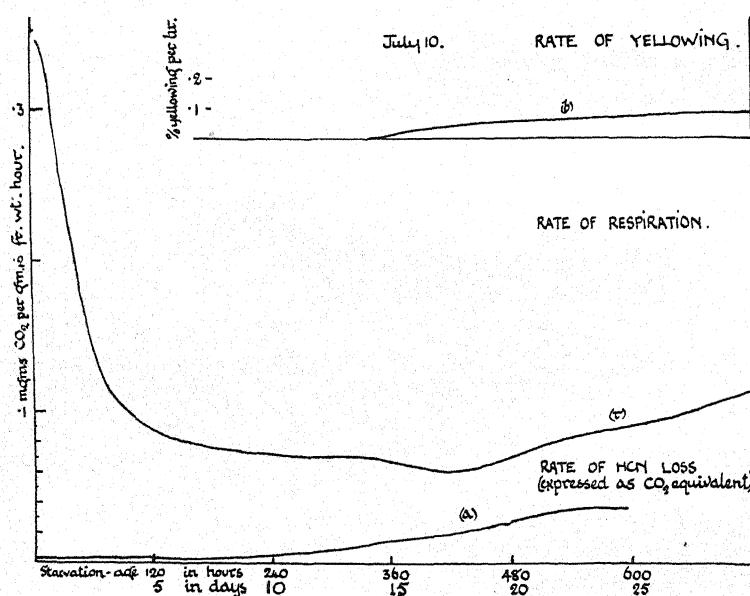
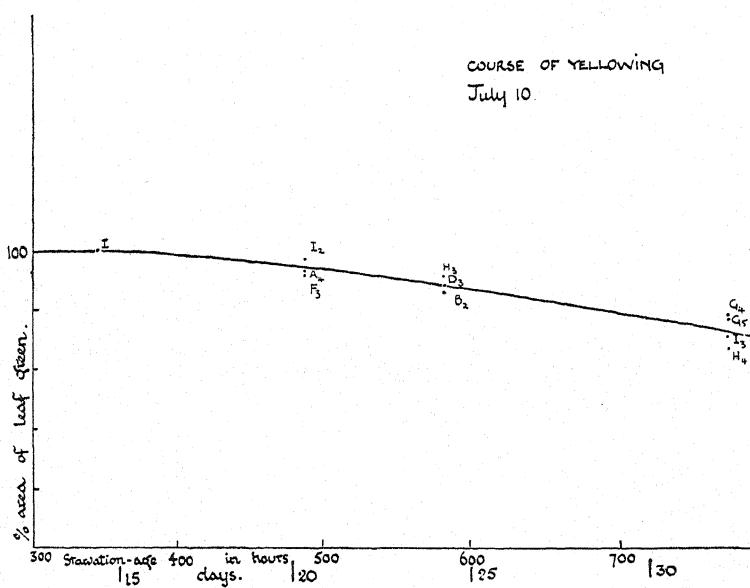
The respiration was determined for two separate sets of six leaves each. The first set (*a*) consisted of leaves from different branches and the second (*b*) of leaves all from the same branch (I_{1-6}). The main stock of leaves consisted of seven sets of six leaves and ten sets of three leaves and on each occasion one of the sets was analysed. The stock was kept in three separate sealed containers in the constant temperature bath; two of these were of brass and the third of glass (covered so as to be light-proof).

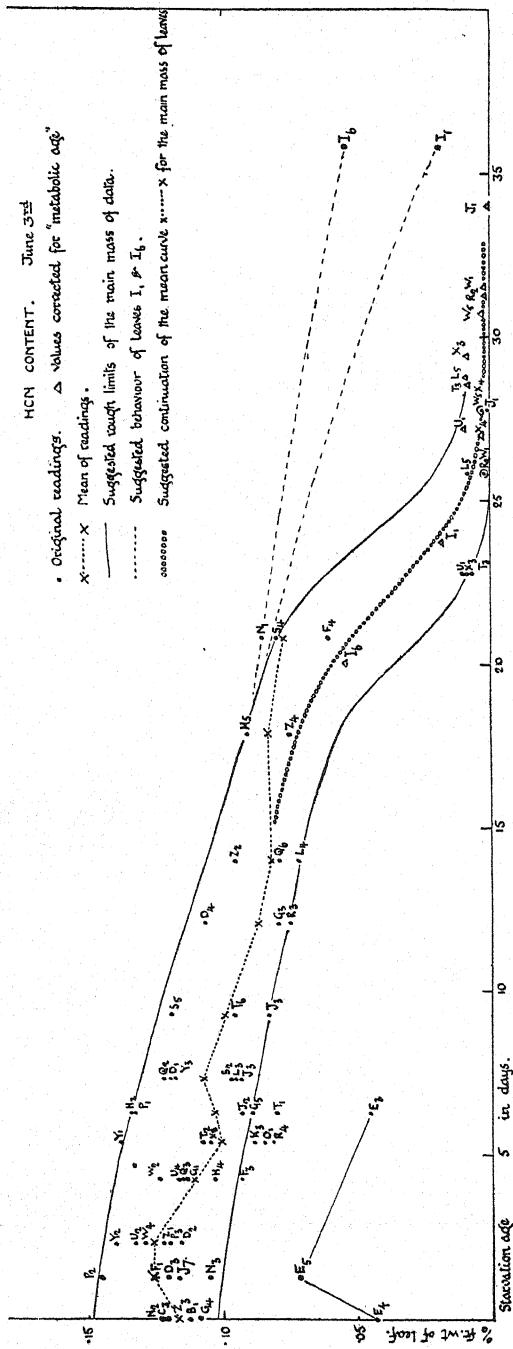
The sets of six were analysed at the beginning of the experiment at intervals of one or two days and the sets of three were analysed at longer intervals during the later part of the time.

Graph 12, showing the glucoside content, has some remarkable features. All the points in the first 500 hours fall within a broad slightly falling band, except a set of three points lying very much below this band which represent the values for leaves E_4 , E_5 , E_3 . This is a more striking instance of the relationship between leaves



Graph 9





from the same branch seen in the last experiment. Further instances of the same phenomenon can be found within the band.

I_1 and I_6 are very slow in their metabolic ageing as shown by the HCN curve. All the individuals of this branch are slow in yellowing and the respiration hump r_1 , Graph 14, is much delayed beyond that of the average set r . The fortunate chance choice of this set for respiration measurement shows, what has not been apparent before, that individuals which are late in yellowing and HCN loss have also a delayed respiration hump.

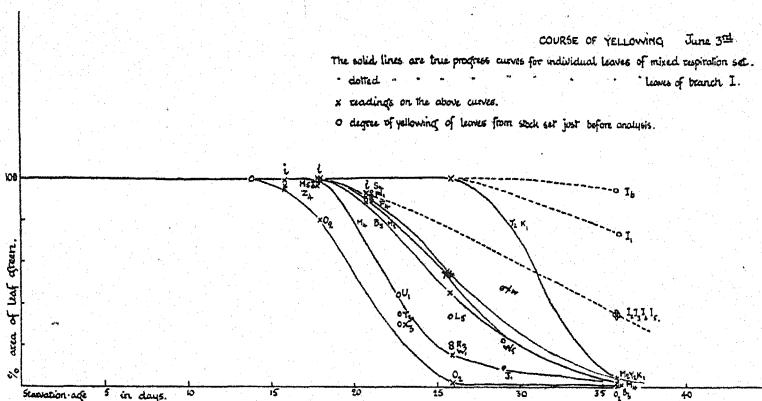
In the yellowing graph (13) the curves drawn are true progress curves from observations at intervals on the leaves in the two respiration sets. The continuous lines are those of the mixed respiration set and the dotted lines from the leaves of branch I . These clearly bring out the wide variations in behaviour of leaves of this age. The points from the analysed leaves of the stock set fall within the region of the rapidly yellowing set. The median yellowing curve of the rapidly falling set has been plotted as a rate curve b , Graph 14, and that of the leaves I_{2-5} as b_1 . The similarity in behaviour of these with their respective respiration curves r and r_1 is clear.

There is no clear indication of the course of HCN loss over the rapidly falling part, Graph 12, since apparently several sets of samples of the slowly falling type precede several sets of the rapidly falling ones. This is borne out by the corresponding yellowing points. The suggested course of rapid fall is indicated ooooooo. It will be seen that I_1 and I_6 corrected for metabolic age fall near this line. Owing to the doubt about its course the latter part of the smoothed curve of HCN loss has not been plotted as a rate curve of glucoside loss. The mean curve of the initial part has been plotted, curve a , Graph 14. It seems probable that the fluctuations are attributable to sampling error so that all this curve indicates is some loss before the commencement of yellowing.

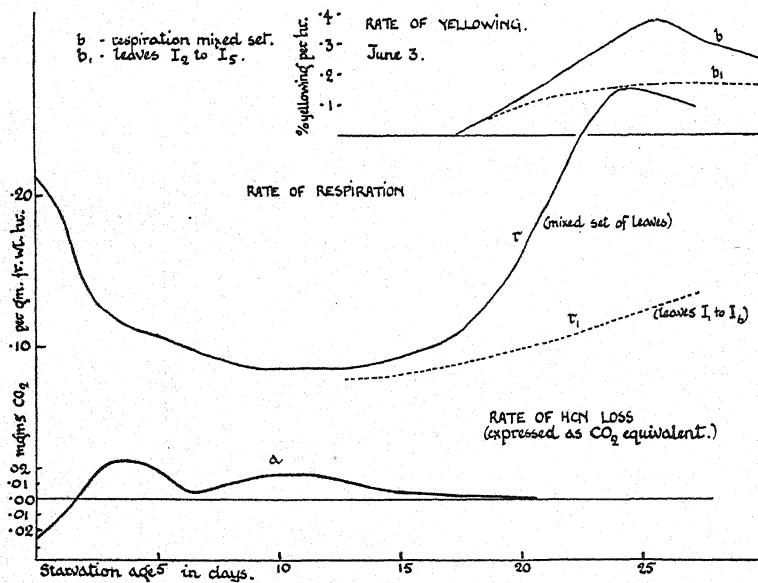
The mean curves for HCN content with time for all four experiments have been plotted together on Graph 15 together with that from a preliminary experiment with leaves $6\frac{1}{2}$ months old. This experiment was complicated by frosting of the leaves immediately before picking. It was found that frosting increases the HCN content of leaves as has been shown for *Sorghum*¹. The initial values in this experiment are much higher than in the others.

The initial contents of the leaves of other ages are close together. It is clear that the younger the leaf the further is delayed the onset

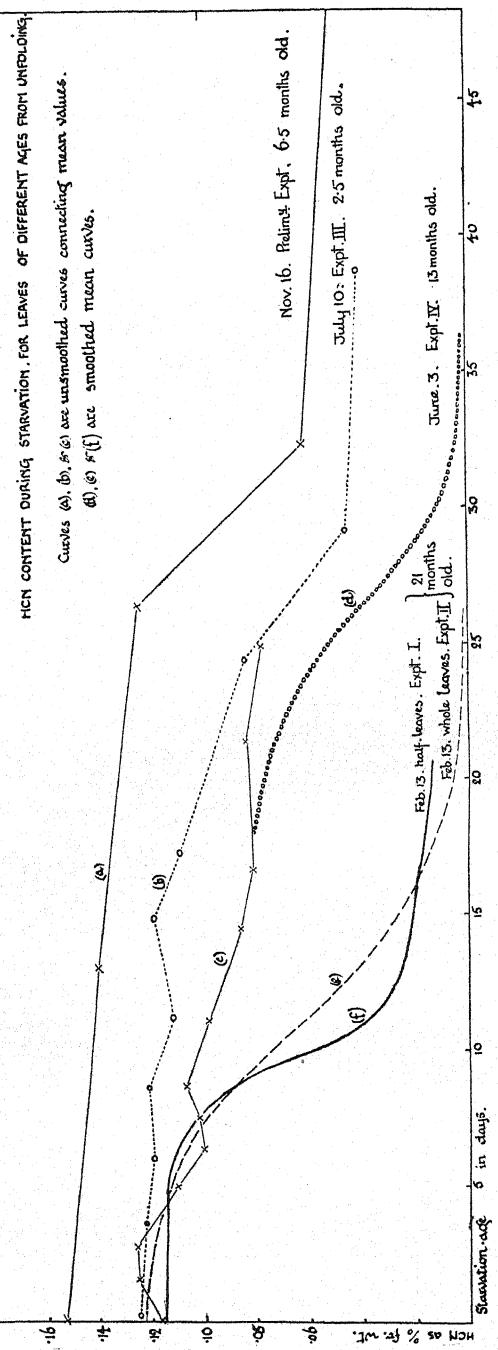
¹ Willamen, *Journ. Biol. Chem.* **29**, 1917.



Graph I3



Graph I4



of the rapid fall in HCN which corresponds with yellowing. The data are not sufficient to establish the point adequately but it seems probable that with leaves of greatest age the pre-yellowing loss of HCN goes on most rapidly.

A GENERAL CONSIDERATION OF GLUCOSIDE BEHAVIOUR.

It is clear from most of the records in the literature of the parts of plants in which glucoside has been found abundantly that these are also the places where there are the other upgrade products of metabolism such as starch. Guignard has demonstrated¹ that cyanogenetic glucosides occur in the leaves of vigorous shoots, young bark and unripe fruits of *Sambucus nigra* and *Ribes*. These are the places where condensation is going on. In very young leaves of cherry laurel about the time of bud opening the percentage content of HCN is very high²: this falls later with the period of maximum growth to a low value. On the other hand the leaves of cherry laurel and of other plants lose their glucoside rapidly during yellowing, and an examination of sections will show that in the yellowed parts of cherry-laurel leaves kept in the light all the starch has hydrolysed although the green parts of the leaf may still be densely packed with it.

Bearing these facts in mind we propose to neglect the teleological explanations of glucoside behaviour which have been advanced so far (for a summary of these see Haas and Hill, 1, 170 *et seq.*). It seems to us much more enlightening to regard the cherry laurel leaf protoplasm as an organisation in which are the necessary enzymes and substrates and protoplasmic conditions for the production of cyanogenetic glucosides. The amount of glucoside will then be seen to be governed by the protoplasmic conditions, and according to the law of mass action by the substrate concentration.

In cherry laurel leaves starving in the dark we have distinguished two phases.

In the first phase the metabolism is that of the mature green leaf in which the available sugars are being used up so that the hexose concentration falls. This fall has been demonstrated by determinations of the hexoses throughout starvation by the Hon. Mrs Onslow (H. Godwin, Thesis). With the removal of one of the factors of the equilibrium there is a tendency for the breakdown of glucoside and other complicated molecules in a manner analogous to enzyme

¹ *C. R.* 141, 1905.

² Rosenthaler, *Bio. Z.* 134, 1923, 321.

hydrolysis *in vitro*. This fall in hexose concentration is reflected, as would be expected from the law of mass action, in a fall in the rate of respiration.

The second phase, that of senescence, is distinguished to the eye by yellowing. In this there is a profound departure from the metabolism of the mature leaf. This change is ascribed to a change in the protoplasmic organisation. The general tendency here is for downgrade metabolism to predominate. One of the resulting hydrolytic actions is the destruction of chlorophyll. The hydrolysis of starch at the same time may be demonstrated by staining sections in iodine and the coincident disappearance of glucoside has been shown both by determinations of the glucoside sugar by Hon. Mrs Onslow and in this paper by determinations of the HCN content of the leaves. The result of these hydrolytic actions is a rise in the hexose concentration. This rise has also been demonstrated (Mrs Onslow, H. Godwin, Ph.D. Thesis). There seems to be no reason why the glucose arising from the breakdown of glucoside should behave in any different manner from that produced by the breakdown of starch, and the result of this rise in the hexose concentration is a rise in the respiration rate until these temporary supplies are exhausted.

The three main phases in the life of an organ are shown in the balance of the upgrade and downgrade metabolisms, the juvenile when synthesis predominates, the mature when there is an equilibrium intermediate in character, and the senescent when there is a rapid passage to complete hydrolysis.

Some possible clue to the explanation of these very complex phenomena may be found at a later date in the colloidal condition of the protoplasm. In the juvenile stage the protoplasm is in the gel state¹ and the available water at the enzyme centres may be presumed to be small so that condensation predominates. In the mature stage the protoplasm is balanced between the states of sol and gel. While in the senescent stage passage to the sol condition liberates the hitherto partially bound conditions of the water and enzymes so that a rapid attack on the elaborated products goes on. Amongst others the glucosides are here broken down.

¹ Stiles, *Permeability*, 1924.

SUMMARY

(1) The methods are described by which a simultaneous study was made of respiration, yellowing and cyanogenetic glucoside content of cut cherry laurel leaves starving in the dark.

(2) From the results obtained the following conclusions are drawn:

- (a) During starvation cyanogenetic glucoside disappears.
- (b) Two separate types of loss may be distinguished, a slow loss in the green parts and a rapid loss on yellowing so that the yellowed parts have no glucoside.
- (c) The period of maximum loss of HCN coincides fairly well in time of initiation, duration and intensity with similar maxima in the rates of yellowing and respiration.
- (d) The initial contents of HCN of the leaves of different ages are fairly close together. The younger the leaves the smaller is the rate of glucoside loss before yellowing and the longer is the time of commencement of the rapid loss postponed.

(3) These phenomena are correlated in a general hypothesis of protoplasmic behaviour.

METHODS OF OBTAINING TRACHEAL SAP
FROM WOODY PLANTS

By J. P. BENNETT, F. G. ANDERSEN AND Y. MILAD

THE sap in the tracheae or tracheids of woody plants is known to be a dilute solution of inorganic and organic materials. Our present knowledge of the nature of the tracheal sap is, however, very meagre. This seems to be due to the inadequacy of the methods of obtaining it. Most of the studies made upon tracheal sap have been with that obtained from plants which show bleeding in the early spring. This gives information on the nature of the sap limited to a single season and to relatively few plants. An advance was made by Dixon and Atkins⁽¹⁾ who centrifuged short lengths of various woody plants at various times of the year and obtained thereby knowledge of composition of the tracheal contents at different seasons and in different parts of the trees. Little use appears to have been made of this method of extraction beyond the work mentioned. This is possibly on account of certain serious limitations: the yield of the sap is often low or nil, so that quantitative procedure on so dilute a solution is impossible or highly uncertain; the method is relatively expensive, requiring costly equipment and large amounts of materials and time to secure the necessary quantities of sap.

Dixon and Ball⁽²⁾ obtained sap from the vessels of twigs and leaves by placing leafy twigs in a strong cylinder with the cut ends of the twigs projecting, and raising the gas pressure within the cylinder as high as 20 atmospheres. This method has been used more recently by Chibnall and Grover⁽³⁾ in a study of the composition of the sap. They consider the sap which they obtained to have come mainly from the leaves. The method is necessarily limited in application to the easily compressible leaf tissues. The sap obtained appears to have come in part from the vessels of the twigs, in part from the vessels of the leaves and in part from the vacuoles of the living cells of the leaf.

In an attack upon certain problems requiring some knowledge of the nature of the tracheal contents of woody branches, more adequate methods of obtaining it in a pure state and in relatively large quantities were desired. Two methods have been developed which appear to meet the main objections to the use of the centrifuge.

Incidentally, another and more serious objection to the centrifuge method has been found, namely, the difficulty of obtaining a uniform sap. The new methods are: (1) displacement by water; (2) displacement by gas.

Displacement by Water.

The procedure consisted in forcing water at one-half to one atmosphere pressure into one end of a cut branch and catching the liquid expelled at the opposite end. Water entering the tracheae at one end apparently drove their liquid contents before it, accumulating them at the opposite end of the branch and finally forcing them out through the cut surface. By determining the electrical resistance of successive small portions of the expelled liquid it was found to vary relatively little in composition after the first few millilitres until the displacing water began to come through, when the resistance began to rise. The water used for displacement had to be of much higher resistance than the expelled sap in order to give accuracy to the endpoint of displacement. A more satisfactory displacing medium than pure water was a dilute solution of a salt. A 0.02 N KCl solution was used in most cases. With this solution the end of pure sap displacement was indicated by a rapid fall in resistance and the appearance of chloride ion in the emerging liquid.

The results obtained with certain branches are shown in Fig. 1. An initial rise in resistance occurred, apparently caused by the gradual washing away of contamination from the injured cells at the cut surface where the sap emerged. This was lessened by a preliminary washing of the cut surface with distilled water, and disappeared after the first few millilitres of sap had emerged. After the initial rise the resistance remained nearly uniform until the displacing liquid began to appear, then fell, or rose, rapidly. MacDougall (4) applied a method similar to this in studying water movement in Pines, by standing small trunks 2-5 metres long in water or coloured solutions and reducing the pressure at the upper end, through a small tube inserted in the wood and connected with an exhaust pump. He found that 60-90 millilitres of sap per hour could be extracted. The composition of this extract was not stated.

Displacement by Gas.

It is well known that gas at relatively low pressure will pass readily through portions of tracheae containing no cross-walls. When gas under pressure is applied to one end of a long cut branch it appears that the gas passes into the opened tracheae, driving the liquid

contents before it and forcing them out through the permeable cross or side walls into other tracheae. This ceases when a cross-wall is reached because the moist walls are relatively impermeable to the gas. If now a section of the branch at the end where the gas is applied be cut off, thereby opening other tracheae to the entrance of gas, their liquid contents may be forced forward in the branch as

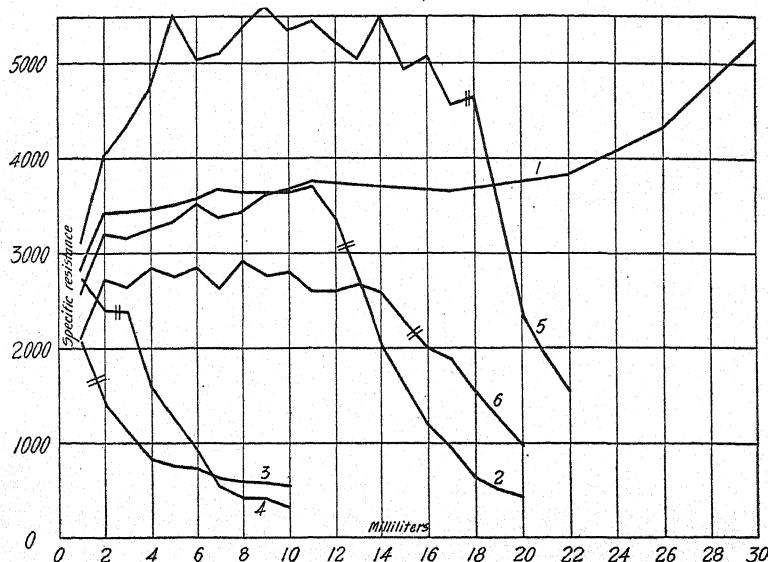


Fig. 1. Sap displaced by water in 1 millilitre portions. Branches used: length 125 cm. diameter, base 2 cm., tip 1 cm., weight 500-800 gm. On each graph // indicates the appearance of chlorine.

Graph No. 1. Pear, displaced with conductivity water.

“ 2. Pear, displaced with N/50 KCl.

“ 3. Peach “ “

“ 4. Apricot “ “

“ 5. Apple¹ “ “

“ 6. Pine^{1, 2} “ “

before. If this operation be repeated several times the liquid tracheal contents will be accumulated in the remainder of the branch and finally begin to be expelled at the end of the branch opposite to that at which gas is applied. By further repetition of this procedure a large proportion of the tracheal sap can be forced out. A practical arrangement of the apparatus consists in placing one end of the branch in a suction chamber and utilising atmospheric pressure to

¹ Resistances should be multiplied by two.

² Amounts of sap should be multiplied by two.

force out the sap. The end of the branch under pressure is now easily cut off in short sections. The suction chamber is so arranged that the emerging sap may be caught in replaceable tubes in any desired quantity. The arrangement is shown in Fig. 2.

The specific resistance of successive portions of sap extracted by this method is shown in Fig. 3. The initial rise in resistance shown by the graphs appears, as in displacement by water, to be due to contamination from the injured cells at the cut surface. In both the gas and water displacement methods much of the contamination,

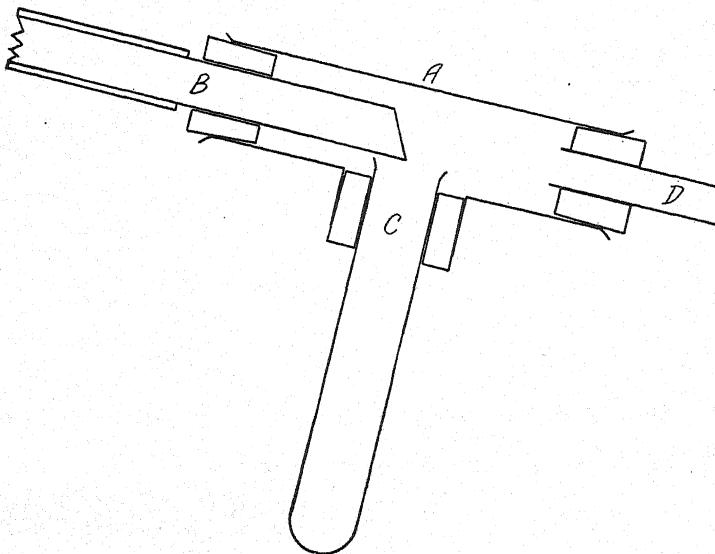


Fig. 2. Apparatus for displacement of tracheal sap by air. *A*, Heavy glass T. *B*, Branch. *C*, Collecting vessel. *D*, To exhaust pump.

causing lower resistance in the first portions of sap emerging, was found to come from the bark. When this was removed and the wood trimmed with a sharp knife so that the sap dripped from the wood without touching the cut edge of the bark the initial lowering of resistance was much less. After this initial contamination has been washed away the sap has practically uniform composition to the end of the extraction process. The distinct advantage of the gas displacement over the water displacement method is the absence of possible mixing with a displacing fluid. A disadvantage appears in that the reduced pressure to which the emerging sap is subjected causes the loss of some of the dissolved gases, chiefly carbon dioxide.

The gas displacement method is applicable to any wood having tracheae a few cm. long. Actually it is possible to use it with wood of shorter vessel-length but it was found to be impracticable with conifer wood. Pine gave no yield of sap at all and redwood gave but 1-2 millilitres from branches 2 cm. in diameter at the base and 125 cm. long, while similar branches of pear, apple and apricot gave yields of 10-25 millilitres. The water displacement method worked

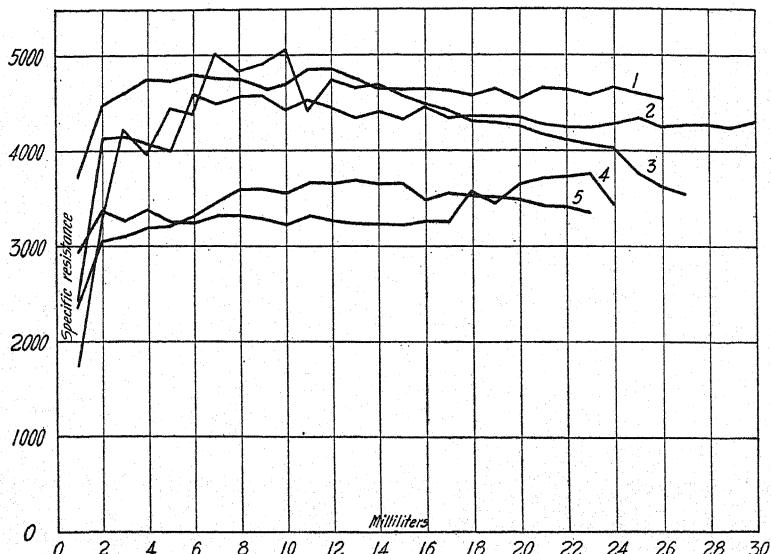


Fig. 3 Sap displaced by air in 1 or 2 millilitre portions. Branches used: length 150-200 cm., diameter, base 2-3 cm., tip 1 cm., weight 800-1500 gm.

Graph No. 1. Peach, yield 52 millilitres.

 " 2. Apricot, " 30 "

 " 3. Apple¹, " 54 "

 " 4. Prune, " 24 "

 " 5. Pear, " 46 "

well with conifer wood, yields of 20-30 millilitres of uniform sap being obtained from pine and redwood branches 2 cm. in diameter at the base and 125 cm. long. With apple, pear and prune branches of similar size, yields of 10-15 millilitres of uniform sap were obtained. With apricot and peach branches somewhat larger and longer, however, the displacing solution began to appear in the emerging liquid in the first to fifth millilitre. This was found to be due to the greater length of tracheae in the latter branches. The longest open tracheae

¹ Resistances should be multiplied by two.

in the apple, prune and pear were from 30-60 cm., while those in the peach and apricot were 90-120 cm. long. Since tracheae with fewer cross-walls in a given length offer less resistance and allow a more rapid flow, the longest tracheae appear to determine the earliness of appearance of the displacing fluid. It is probable that in the water displacement method most of the uncontaminated sap comes from the largest and longest tracheae which offer the least resistance to flow. In the gas displacement method, however, the displacement of sap probably occurs from all opened tracheae since the gas would flow readily into the smaller tracheae. Both methods are applicable to branches or roots of any size or length and of high or low water content, with the limitation mentioned above as to length of tracheae, so that large amounts of sap may be obtained in a relatively short time.

It has been found possible, using the gas displacement method, to separate sap from different annual rings of the wood, or even to separate sap from inner and outer vessels within a single annual ring. To accomplish this, metal tubes of suitable size were driven into the end of the wood at which the sap emerged, so as to keep separate the saps from the different regions and deliver them into separate vessels. The arrangement of apparatus for this purpose was essentially the same as shown in Fig. 2 except that a wider opening at C received a stopper holding two or more receiving vessels.

The Centrifuge Method.

In comparative tests the centrifuge method was found to have serious shortcomings. The yield of a prune branch 2 cm. in diameter at the base and 125 cm. long when cut into 15 cm. lengths and centrifuged was found to be only 2 millilitres total in contrast to yields of 10-30 millilitres by the other methods. Further, when the soil about the tree was low in moisture, it was frequently impossible to obtain any sap by centrifuging, until after irrigation, thus seriously limiting the usefulness of the method. Dixon(5) reports relatively larger yields than obtained here, by centrifuging from beech and poplar wood at different seasons. Different woods appear to yield different amounts of sap. Pear or prune wood in our experience always yielded more sap than apricot. Certain woods like pine and redwood have yielded little or no sap on centrifuging at any time. The amount of contamination from cut surfaces is greater in the centrifuge method than in the other methods because of the necessity of cutting the wood into relatively short lengths, thus

increasing the number of contaminating surfaces. And it is impossible to separate the contaminated first portion of the expelled sap from the purer later portion in centrifuging.

A still more serious objection to the centrifuge method lay in the variation in the concentration of the sap obtained with different speeds of the centrifuge. With increased speed a sap showing a lower specific resistance was obtained, and at the lower speeds the sap obtained often had less resistance than sap obtained by either water or gas displacement. The lower resistance of centrifuged sap was most probably caused by contamination from fragments detached from the surface of the branch during centrifuging. Removal of the bark always gave a sap of lower resistance than with the bark left on. Washing the surface before centrifuging decreased the contamination. The centrifugal force exerted by the centrifuge used in this work was approximately 1000 times gravity at 2400 R.P.M. It is possible that the high pressures imposed on the tissues during centrifuging may have caused some leakage of substances into the tracheae from the surrounding living cells. The lowest speed at which sap could usually be obtained was about 1000 R.P.M., but varied with the variety of tree and with its water content. A general comparison of sap obtained by the three methods is given in the table.

Specific resistance of tracheal sap displaced by

Tree	Ex- press- sap	Gas	Water	Centrifuge		Remarks
				Low speed 1000-1500	High speed 2500-3000	
Prune	321	4000-4400	—	3570-4200	—	Same branch
	—	—	—	5160-5370	3640-4660	Halves of same branch
	—	—	4000-4600	3000-3500	—	Bark on
	—	—	—	800-1200	—	Bark off
Pear	200	—	3200-3800	2300	—	Same branch
	—	3900-4200	—	—	—	
	—	—	—	3270	2610	Half of same branch
	—	—	—	4170	3150	" "
	—	—	—	4330	3810	
Apricot	260	4100-4600	a	1800	—	Different branches
Peach	—	4500-4900	a	—	—	
Apple	—	8000-10,000	9000-11,000	—	—	Different branches
Pine	—	b	5400-6100	b	b	
Redwood	—	4200-4450	4900-5500	b	b	Different branches

Specific resistance: distilled water 13,000; tap water 2500; 1 : 1 soil extract 4800-5800.

a Contaminated with displacing fluid.

b No sap obtained.

As the data in the table and figures show, the sap from the tracheae was a very dilute solution. It was in most cases roughly comparable in concentration with the laboratory tap water or a 1 : 1 water

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extract of the surface soil in which the trees were growing, and usually considerably more concentrated than the laboratory distilled water. The ions found in it were Ca, Mg, Fe, K, PO₄ and NO₃, and HCO₃ in some cases. The non-electrolytes detected were reducing substances, probably sugars in part, sucrose, amino acids and amides. The reaction of the tracheal sap, when allowed to reach equilibrium with the air, varied with the soil in which the trees grew. On acid soils it has been found to range from pH 5.5 to pH 6.4. On soils rich in lime it was found to be pH 7.0-7.2 and on expelling the CO₂ present by heating was as high as pH 8.0. The reaction of the sap, while still in the vessels, was not determined but is probably kept somewhat acid, even when carbonates are present, by the relatively high CO₂ concentration present. Quantitative studies on the composition and reaction of the tracheal sap at different seasons are being carried out in this laboratory.

The methods of obtaining sap described afford a point of attack on many problems, particularly those of nutrition, which has hitherto been at least not readily attainable, and practically undeveloped. It seems probable that studies of the tracheal sap will throw light on such problems as absorption and utilisation of substances from the soil, sap-flow, root-pressure, transpiration and translocation of organic and inorganic compounds, at least in woody plants. It is hoped to extend the method to many herbaceous plants.

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SYNTHETIC DYESTUFFS AS MICROSCOPICAL STAINS

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THE use of synthetic dyestuffs in microscopy still rests largely on an empirical basis. The practice arose about 1865 as a natural offspring of the coal-tar colour industry. This industry had its beginnings in the years 1856-60, and its products were brilliant colouring-matters with quite novel properties. But whereas the manufacture of dyestuffs has continued ceaselessly to develop in the sense that new chemical combinations are always, nowadays as actively as ever, being produced to satisfy the more and more stringent demands of the dyer, the application of artificial dyes in microscopic technique has remained almost at a standstill, as far as widening the range of dyestuffs used is concerned, since about 1890. This is unfortunate; it is probable that the histologist is unknowingly limiting himself; and the botanist, in particular, may suffer in this way because he has not had the same interest in the chemical side as has, for example, the pathologist. It is not, however, the aim of this note to suggest additions to the range of stains, already formidable enough from some points of view, but to indicate likely sources of misunderstanding and error that may arise when the present more or less familiar selection is in use.

What is implied in the above is that, on chemical grounds, the dyes at present in use as stains are not altogether satisfactory. This point will be dealt with later; there are other causes of confusion and error. There is the question of nomenclature: the names of dyestuffs are, or were originally, trade-names, i.e. trade marks; they have little or no connection with orthodox chemical nomenclature. Moreover, when a dyestuff is made by a number of manufacturers, each maker names it as he pleases. So it comes about that a single dye-stuff, well defined chemically, may have a dozen or so different names, whilst the same name, qualified by letters added as suffixes, may be applied to several chemically different dyes. For example, orange-G and orange-II are chemically distinct, but magenta and fuchsine are identical. Usually the oldest name has been adopted in micro-technique, but this multiplicity of synonyms leads to much confusion. In Strasburger's well-known textbook(1), for example, and in papers in this *Journal*, the use of bismarck-brown and of vesuvine,

as if they were different stains, is described, whereas these names are synonymous. Moreover, Strasburger (*loc. cit.*) includes in his shortest list both methyl- and gentian-violet, yet it is doubtful whether, even before the war, when practically all the stains in use came through one German marketing concern, there was sufficient difference between these two substances to justify their being given each its own technique.

Confusion also easily arises between such names as aniline-blue and aniline-blue water-soluble, and magenta and acid magenta. The first of each of these pairs is a "basic" dye, the second an "acid" dye, that is, their staining properties are radically different, but this question will not be discussed here. Similarity of names for quite different products, for example, methyl-blue and methylene-blue, may also give rise to misunderstanding.

The confusion due to the clumsy nomenclature is aggravated in that certain names are unknown except as applied to the stains. Thus, gentian-violet is not known as such in the dye-trade, and aniline-green has long been obsolete¹. This stain, it may be noted, is mentioned by numerous authors, but it is not easy to discover which of two early dyestuffs, both called by this name, is meant, and its use should be abandoned. Worse than the above, however, is an apparent tendency to introduce, for some obscure reason, special trade names even into this limited field: thus, an important marketing-house is now issuing safranine² both as such and under the name "gossypimine."

Much, if not all, of this confusion can be avoided by consulting a standard reference book on dyestuffs. The Society of Dyers and Colourists' *Colour Index*⁽²⁾, which has been compiled since the war, is comprehensive, and has special notes on many dyes used as stains, but the older tables of Schultz and Green⁽³⁾ give most of the essential information. An attempt has recently been made by an American committee to condense the literature on stains and staining into a book⁽⁴⁾. This book should prove very useful, but unfortunately it is marred by misleading and sometimes even erroneous statements, particularly on chemical questions. As far as nomenclature is concerned it is fairly trustworthy. A critical account, superior to many others, is given by Langeron⁽⁵⁾.

¹ Cf. Ehrlich's *Enzyklopädie der mikroskopischen Technik*, 1903.

² "Carthamine" or "Carthamin," strictly the name of the colouring matter of unknown constitution present in safflower, has also been a trade synonym for safranine, and "Carthamine-B" is "rhodamine-B".

Conn (4) and Langeron (5) draw attention to the fact that stains are commercial dyestuffs which may or may not be specially purified. A dyestuff is almost never put on the market as 100 per cent. chemically pure. Usually, for various reasons, it is "let down" with some suitable inorganic (common salt, sodium sulphate) or organic (dextrin) diluent. Inorganic salts will almost always be present; dextrin may be, but only in basic dyes. Preparations sold as stains may be specially purified¹; in any case, as staining solutions are made up on an empirical basis, the exact strength is almost a matter of indifference, but the fact that up to 50 per cent. of the solid stain may be inorganic electrolyte may be of importance in special work.

Another important cause of possible confusion may lie in this, that many of the dyes used as stains are not individual chemical compounds. Particularly in its early days, the synthetic dye industry worked on an empirical basis. Safranine, methyl-, gentian-, and crystal-violets, aniline-blue, and so forth were all regularly manufactured and used before their chemical composition had been elucidated. It is now known that these, and many others, are by no means chemically homogeneous. To the dyer this is a matter of indifference, but as these dyes are now being used not only for simple staining, but also as reagents to elucidate physiological questions, it may become a matter of importance to the histologist.

Although these mixtures are generally of chemically similar compounds, the exact composition of some is not yet known. Nigrosine (spirit-soluble), for example, is a complex mixture of reddish violet and bluish violet isomeric and homologous compounds; the water-soluble brand is this mixture sulphonated far enough to yield water soluble sodium salts. Magenta is similarly a mixture, so is bismarck-brown. In fact, of all the synthetic stains listed by Strasburger (1), only eosin, orange-G, and delta-purpurin are likely to be chemical individuals. Light green SF and gold-orange, included in Chamberlain's list (6), are also homogeneous products.

The foregoing notes will demonstrate the importance of attention to nomenclature in using stains, and will suggest that caution is necessary when purchasing them. Whether efforts to standardise supplies, in the manner proposed by Conn and his collaborators (4), are justified, is perhaps doubtful, but it would surely be an advantage if users of stains familiarised themselves with the information given

¹ But cf. Zimmermann-Schneider, *Die Botanische Technik*, Jena, p. 122. 1922.

in such a volume as the *Colour Index*, and quoted its numbers when necessary.

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SYMBIOSIS AND ASYMBIOSIS RELATIVE
TO ORCHIDS

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WITHIN recent years the germination of orchid seed has been investigated by a number of individuals and to these have been added comments by various others. Differences of opinion prevail as might be expected. This is of no great consequence since it is only a question of time when the disputed points in regard to the physiology of orchid seed germination and the significance of symbiosis in orchids will be firmly established. But in a number of these papers certain deductions are drawn that are misleading and certain comments are made relative to my investigations and conclusions that require some consideration and in some cases necessitate refutation. Personally I have no desire to enter into a controversy concerning the physiology of orchid seed germination. Advances in our knowledge of the physiology of orchid seed germination can best be attained by continued investigations rather than by mere speculation.

Clement (5, 6, 7) has recently published three papers on the asymbiotic germination of orchid seed. His figures clearly show that he has been as successful as he states in the germination of orchid seed but he is less accurate in some of his statements. In regard to the importance of the hydrogen-ion concentration Clement (7) p. 165) states that he was the first to point out that attention should be given to this. Priority is not a matter of great importance but it may be stated that in April 1924 I called attention to the desirability of giving consideration to the hydrogen-ion concentration and emphasised this especially in 1925. The latter paper, of course, appeared subsequent to Clement's 1924 papers. A matter of very great importance is the conclusion of Clement in regard to the hydrogen-ion concentration that should prevail in the culture medium for asymbiotic germination. He (6) p. 359) states the following: "As previously pointed out the hydrogen-ion concentration of the medium is important, and tests made go to show that from seeds of the above genus (*Odontoglossum*) the ρ H value most suitable needs to range between 6.5 and 6.8, other factors in the composition being satisfactory. It is possible that the solubility of

food materials contained in the substratum is influenced by the pH value, notably phosphates; also, to some extent, processes of conversion may be affected." Again in 1926 Clement (7) emphasises the desirability of maintaining a pH value of between 6.5 and 6.8 for seed of various genera.

This may be the optimum range of hydrogen-ion concentrations for the solution that Clement is using but the statement is not only worthless to those interested in germinating orchid seed but actually misleading if use is to be made of any of the published formulae. Unfortunately Clement has not published the formula of his nutrient solution. So far as I am aware only Bernard (2), Burgeff (4) and I (12, 13, 14) have published the details of our methods and the formulae for culture media. It may be confidently stated that if any of the solutions of Bernard, Burgeff or myself are used very poor results will be obtained if the hydrogen-ion concentration is maintained between pH 6.5 and pH 6.8. With my solution B, which I have repeatedly used, or with most nutrient solutions in use, the hydrogen-ion concentration should be close to pH 5. We have made various investigations in our laboratory on the relation of pH to plant growth and shall soon publish on the relation of pH to the growth of orchid seedlings. Suffice it to say here that when the nutrient medium has a pH of 5.5 or higher both phosphates and iron may be precipitated. With the precipitation of iron the seedlings become yellowish green and if the pH is close to 6.6 with my solution B, then the seedlings are almost white in colour. The precipitation of the iron is due in part to the formation of ferric hydroxide and in part to adsorption of iron by some of the precipitated phosphate (Hopkins and Wann (11)). It may be pointed out furthermore that most of our native orchids grow under slightly acid conditions (Wherry (16)) and it may also be concluded that the seedlings of epiphytic orchids in the tropics are never subject to a hydrogen-ion concentration higher than pH 6. Very likely the reaction about the embryo is more acid than pH 6. The fact that Clement had to devise different solutions for closely related species indicates that he was using a hydrogen-ion concentration which was just at the border line between keeping the iron available and precipitating it.

Clement, presumably referring to some of my experiments and conclusions, makes a number of statements that require contradiction. In 1924 I published an account of *Cattleya* seedlings that had been grown with sugar and when the leaf point was just appearing the seedlings were transferred to a nutrient medium containing no sugar

but only agar to produce the semi-solid substratum. This experiment was designed to prove that the orchid after the first month or so is capable of synthesising its own food and is therefore independent of any outside organic food. Clement (6) p. 360) asks: "In instances where *Cattleya* seedlings in an advanced stage of germination have been transferred to a medium of Pfeffer's solution, plus agar, is it not conceivable that by reason of the presence of agar, which being a carbohydrate substance containing a mono-saccharose, e.g. galactose, that some slight organic matter may become available to the seedlings after they have developed true roots?" That the above medium is of no value for the complete germination of seed has been proved by many experiments. Furthermore, assuming that galactose is present, and this is hardly probable, it would be of no value. In a rather extensive investigation (not yet reported) on the use of various sugars by orchids, I have found that galactose is not used.

Again Clement (7) p. 168) states without mentioning my name that "it has been suggested by another investigator that the virtues of the endophyte are due chiefly to its secretion of acid." The significant facts in this connection developed in my 1925 paper are that the fungus when added to the culture changes the starch to sugar and produces a favourable hydrogen-ion concentration, one which keeps the iron available for the embryos. The effect of the fungus can then be ascribed entirely to changes induced in the culture medium.

Drs G. and M. Ballion (1) in the *Orchid Review* have presented a general summary of some of their experiments without giving the nutrient solution employed. They report the usual satisfactory germination with asymbiotic methods. Inadvertently perhaps and certainly somewhat inconsistently with the views expressed by them as regards the normality of plants with and without the fungus, they seem to incline to the view that the germination asymbiotically is induced by a stimulus comparable to that in artificial fertilisation. It cannot be over-emphasised that there is nothing particularly mysterious in the stimulus to germination by the appropriate nutrient solution. Orchid seed will not germinate without organic matter of suitable character. If a purely mineral nutrient solution is supplied and a non-utilisable sugar is added then there will be no germination, no matter what the concentration of sugar. If to such a culture the fungus is added then germination still is prevented, but add the appropriate sugar, any sugar that can be utilised by

higher plants such as glucose, fructose, xylose, maltose, or sucrose, then germination occurs. The sugar is used as a food and exerts no mysterious physical chemical stimulus as has been implied. When the fungus is used germination is possible because of the action of the fungus on the culture medium. When starch is supplied this is changed to sugar and if other insoluble organic matter is provided such as *Osmunda* fibre it too is partially converted to sugars.

Constantin⁽⁸⁾ has just recently published another theoretical contribution to the subject of symbiosis and asymbiosis in orchids and, as previously, seems to consider it necessary to deal in a rather ungracious manner with those who differ from him. Constantin criticises Clement, Drs Ballion and myself for questioning obligative symbiosis as a requisite for "normal" seedlings and plants. Clement on this subject has adopted no positive view relative to the function of the fungus. Drs G. and M. Ballion have very appropriately taken issue with those who predict that plants grown from seed germinated asymbiotically or plants grown asymbiotically will not flower. It is probably true that there are at present no well authenticated cases of orchid plants (other than species of certain genera that do not have the fungus) that have been brought to the flowering stage asymbiotically. This is very probably due to the fact, as Mercier⁽¹⁵⁾ and Constantin have indicated, that the orchid fungi are widely distributed and without extreme precautions it would be difficult to prevent infection. Bultel⁽⁸⁾ reports flowering of plants raised from seed germinated asymbiotically but the plants became infected subsequent to transfer to pots. Four of my *Cattleya* seedlings have flowered normally at the age of five and one-half years. These plants had been maintained in flasks under asymbiotic conditions for the first year and then transferred to pots with *Osmunda* fibre. Although kept in a greenhouse in the absence of other orchids they became infected. Of course Constantin would state that these plants flowered only because they became infected and the infection induced the production of vitamines essential for reproduction in plants. These statements of Constantin have no scientific importance for the statements merely give expression to a guess and nothing else.

What is Constantin's evidence for the abnormality of asymbiotic plants? First, is the constancy of association of fungus and orchid under natural conditions? Constancy of association may, however, signify merely that the orchid fungus is widely distributed and that the orchid is readily infected. He refers likewise to the pronounced

effect of the fungus on the nuclei of the infected cells and that ultimately the fungus is digested. He emphasises as did Bernard (2) that the nucleus behaves as a phagocyte in destroying the fungus. Is there any evidence for this view outside of certain nuclear peculiarities observed microscopically? Is it possible to explain this digestion of the fungus merely by observation microscopically? Is it not possible that the fungus cannot penetrate adjacent cells and that ultimately autolysis of the fungus results because of lack of food? Are these abnormalities of any particular significance and are they not paralleled in many diseases of plants? We know that the acceleration of growth of the orchid embryo when the fungus is added results only when the culture medium contains food that is insoluble and therefore unavailable to the embryo. The fungus accelerates growth because it digests the insoluble food and makes it available.

Constantin is so impressed with the idea of obligative symbiosis that it is the only reason that he can ascribe for the failure of *Psilotum triquetrum* to fruit at the Muséum National d'Histoire Naturelle de Paris. This plant was raised asymbiotically and is apparently in fine vegetative vigour, but again it is pure assumption to state that it fails to flower because of lack of the appropriate fungus. *Psilotum triquetrum* is a native of the tropics, usually epiphytic and probably growing with low nitrogen supply. Recent investigations indicate that the carbon-nitrogen relations are important factors in reproduction. Furthermore the work of Garner and Allard (9, 10) on the relation between the relative length of day and reproduction must be taken into consideration as well as other environmental factors.

The constancy of association of fungus and orchid needs re-investigation and particular attention should be given to the epiphytic orchids in the tropics. It is a well-known fact that roots exposed to light and which produce chlorophyll are not infected. In the tropics the roots of orchids clinging to the bark of shrubs and trees are exposed to light and therefore not readily infected. I have already found some plants of a small species of *Oncidium* growing in Guatemala that had produced seeds and the roots were free of the fungus, and it is probable that many orchids will produce flowers under these conditions when they are entirely free of the fungus.

Constantin has emphasised greatly the abnormality of the embryos grown asymbiotically for he states that they always contain starch, whereas the function of the fungus is to digest starch in the

embryo. As evidence that the asymbiotic embryos contain starch Constantin (8) p. vii) quotes me as follows: "Embryos in sugar containing cultures accumulate a considerable reserve of starch." This is a correct quotation but it is only partly true for on page 13 of the same paper (12) I state specifically that starch was present only when the sugar concentration of the culture medium was 0.80 per cent. or higher. In this experiment the concentration of sugar varied from 0.05 per cent. glucose to 2.0 per cent. glucose. In regard to the culture I stated as follows: "On February 15th the embryos of all cultures were examined for starch. It was found only in those cultures with 0.80 per cent. glucose or higher. This fact is evidence that absorption of glucose at a concentration of 0.80 per cent. or higher is in excess of utilization." The fact of great significance repeatedly observed is that germination can be obtained with concentrations of glucose of very low concentration, less than 0.1 per cent. The time for germination is longer, but below 0.8 per cent. glucose starch appears to be absent.

Constantin (8) p. vii) admits that the facts established in my 1925 paper would appear very disconcerting to him were it not for the observation noting the presence of starch in the embryos. (J'avoue que l'ensemble de ces constatations serait assez déconcertant si M. Knudson n'avait pas fait la remarque qui vient d'être citée plus haut (en anglais); tous les auteurs qui ont parlé de l'action du *Rhizoctonia* interne ont justement conclu qu'il sert à dissoudre l'amidon.") This argument by Constantin that the presence of starch is an abnormality would not impress any physiologist as of importance but since the embryos do not contain starch when lower concentrations of sugar are used perhaps Constantin will be somewhat more disconcerted and at least far less positive concerning obligative symbiosis as a condition for normal germination.

Constantin in referring to the possible function of the fungus leaves one in some doubt as to his viewpoint relative to the rôle of the fungus. He states (8) p. vii): "A quoi sert le Champignon? Évidemment à la nutrition de l'Orchidée, puisque cette plante, dans la phagocytose, digère les filaments qui sont en bordure de la zone fongique." Later, however, he states the view expressed previously by others that the function of the fungus is to digest starch in the embryos. This view reiterated by Constantin cannot hold, for even though the fungus enters the embryo there is no starch in the embryo to be digested. I have examined at various times seed of *Laelia*, *Cattleya*, *Cymbidium* and *Odontoglossum* and have never found

starch in the embryos unless sugar had been supplied and as indicated previously not always is starch present with sugar. I have never found starch in embryos developing on a nutrient medium containing only nutrient salts and agar. The reserve food at the outset is largely fat. If starch is present in the embryo it is evidence that sugar has been absorbed from the culture medium.

Constantin (8) p. vii) in discussing the results of my experiments with the orchid fungus invents for me certain deductions which are misleading and which I never made. Referring to me Constantin states as follows: "Je ne puis pas admettre que le Rhizoctone n'agisse pas aussi bien quand il est interne que quand il est externe. D'ailleurs, M. Knudson le prouve lui-même quand il parle de cultures ensemencées de *Rhizoctonia*. Il remarque, comme une chose très importante, que certaines graines, parfois en grand nombre, ne sont pas pénétrées par le Champignon. Il constate, il est vrai, une avance pour celles qui sont envahies: le Champignon en milieu interne a donc une action plus efficace; pour les graines en retard, non pénétrées, c'est encore le Champignon qui a modifié le milieu externe et déclenché la germination." According to this quotation from Constantin, I found that the infected embryos developed more rapidly than uninfected embryos. From this he draws the conclusion that the fungus must have an internal action on the embryo which is beneficial. This would be a convincing argument for obligative symbiosis if true but in none of my papers are there any data or statements which would substantiate the conclusions drawn by Constantin. As a matter of fact I emphasised repeatedly (and the evidence given was fully adequate for the statements) that the change of starch to sugar and the production of a favourable hydrogen-ion concentration explained the favourable effect of the fungus. When the species of *Phytophthora* was used, germination was about as good as with the orchid fungus. The slightly greater growth with the orchid fungus could be explained again on the basis of a slightly more favourable hydrogen-ion concentration. In neither case were the embryos infected. The action of the fungus could not then have been internal.

There is no need here to enter into a detailed discussion of the evidence for or against the view that obligative symbiosis is a condition for seed germination and flower production by orchids. I have taken up these questions in a number of papers and it will be considered again in certain investigations that I expect to report soon. Bernard and others who insisted on the necessity of the fungus for germination insisted likewise on an internal action of

the fungus. My own investigations clearly reveal what had not been hitherto considered, that the changes induced by the fungus in the culture medium are of primary importance. My own work clearly shows the dependence of the orchid embryo on soluble organic matter and the investigations indicate that the capacity for synthesising food is lacking in the embryos of orchids. Decay of organic matter in nature is effected by a variety of micro-organisms both fungal and bacterial. The orchid fungus may of course be one organism involved in this transformation of insoluble organic matter but to state that the orchid fungus alone prepares the organic matter for the orchid embryo under natural conditions is pure assumption.

Constantin emphasises the point that we should not ignore the teachings of nature. Nature presents a set of conditions and the interpretation is made by man. Constantin interprets the constancy of association of fungus and orchids and the nuclear and fungus disintegration as paramount evidence of the necessity of the fungus for the full manifestation of the plant cycle from seed germination to seed production. The constancy of association of fungus to me merely means that the orchid fungi are widely distributed and that orchid embryo and orchid roots are generally readily infected. Furthermore, the fungus may be held in check and the orchid then survives or the fungus may gain the ascendancy and cause death of the plant. Constantin waits impatiently for the demonstration of flower production by plants grown asymbiotically. One wonders why Constantin himself did not attempt to verify some of the views held by himself in respect to the "abnormality" of plants grown asymbiotically. Mere statements based on the "teachings of nature" are not adequate proof to those who believe in the experimental method.

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